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The International Congresses of Entomology

by

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The International Congresses of Entomology appear to have arisen in the first instance as a development of the International Congresses of Zoology of which the first was created in 1889 by the Zoological Society of France. The first Entomological Congress however, came to be through the personal initiative of Dr. Karl Jordan. Dr. Jordan felt that although entomology has a place in Zoological Congresses this was not commensurate with its importance. He considered that entomology was suffering from the absence of a representative organization where entomologists could meet and discuss their common problems. He noted that many important entomological works, large collections and even the name of distinguished specialists remained quite unknown to non-entomological zoologists. He observed that here and there ill feeling had developed among members of the entomological profession to the great damage of biological science. He found that although entomologists were very numerous and had produced a tremendous mass of work a good deal of this had little scientific value. Finally he complained that in Europe, at least, few of the scientific entomologists were at all interested in the insects of importance to agriculture and to health. Some of the colleagues he consulted doubted that an Entomological Congress could be organized but all agreed that it would undoubtedly be beneficial to entomology. Therefore after preliminary conversations on a number of occasions Dr. Jordan wrote in 1906 to some of the foremost entomologists of Europe on the subject and in 1908 a committee was formed having as members A. F. Dixey, G. C. Champion, H. Rowland-Brown, E. B. Poulton, G. A. K. Marshall, W. Horn, A. Janet, G. Severin and K. Jordan. This committee met in the rooms of the Linnaean Society in London and as a result of their discussions Horn, Janet, Severin and Jordan were empowered to act as a Congress Executive Committee. It was decided that the Congress would be held in the first week of August 1910 in Brussels, fifteen days before the Fifth International Congress of Zoology. This arrangement was made so that the zoologists coming either from England or from the United States to the International Zoological Congress could also attend the First Entomological Congress. It was decided also that the First Congress would nominate at its final plenary meeting a Permanent Committee to advance the idea of entomological congresses in all parts of the world. To this end a provisional committee composed of representatives of several European countries was set up. This committee drew up a list of entomologists it charged with the creation of local congress committees in all parts of the world. It is pleasing to read in this list, as the President of the Canadian Committee, the name of one of the great founders of Canadian entomology, the Reverend Dr. C. J. S. Bethune, at that time Professor of Entomology in the Ontario Agricultural College. On the other hand it is interesting to note that although, in 1909, well organized official entomological services existed in both Canada and the United States, the help of the heads of their services was not enlisted. The outlook of the Congress Executive at that time seems indeed, to have been largely academic.

A great effort was made by the Executive Committee in connection with the Congress. The first circular was printed in English, German and French and

45,000 copies were sent out, 15,000 in each language. A second circular accompanied by membership forms and so forth and printed in June 1910 was also sent out in the three languages and 11,000 copies were posted.

The Congress itself opened on Monday, August 1st, in Brussels and closed on August 6th. It was organized in sections devoted to the various aspects of entomology. Although somewhat less than 150 entomologists attended the Congress many others who did not attend became members and the Congress itself was very successful, both socially and scientifically. The President, on this occasion was Professor A. Lameere, at that time President of the Entomological Society of Belgium and Professor in the University of Brussels. The General Secretary was G. Severin of the Royal Museum of Natural History of Belgium. At the opening of the Congress the Executive Committee nominated a number of Honorary Members among whom were J. H. Fabre and Alfred Russell Wallace.

The Second International Congress was held in Oxford, under the Presidency of Professor E. B. Poulton with Dr. Malcolm Burr as Secretary. The attendance was somewhat larger than at the First Congress and there was a rather better representation from Canada and the United States particularly with respect to economic entomology. Seventeen more entomologists were appointed to the Permanent Committee and three more Honorary Members were elected. Plans were made for the holding of the next Congress in Vienna in 1915 but the outbreak of the First Great War in 1914 frustrated these plans. It was not until 1925, thirteen years later, that the Third Congress was organized in Zurich, Switzerland, under the Presidency of Dr. A. v. Schulthess-Rechberg with Dr. A. Pictet and Professor O. Schneider-Orelli, as Vice-Presidents and Mr. H. Kutter as General Secretary. Only two entomologists from North America attended: Professor O. A. Johannsen from Cornell and Dr. L. O. Howard. At this meeting fifteen new Honorary Members were elected. The so-called Permanent Committee made up of a large number of entomologists from all parts of the world had been found to be of no practical value and it was therefore dissolved. At the opening of the Zurich meeting the Executive Committee carrying over from Congress to Congress consisted only of W. Horn of Berlin, K. Jordan of Tring and H. Skinner of Philadelphia. H. Eltringham, Y. Sjöstedt and R. Jeannel were added to this committee.

The Third Congress left the selection of the country of the meeting of the Fourth Congress and the election of the President in the hands of the Executive Committee. There was a strong general desire to hold the Congress in the United States but it seemed uncertain whether, in the aftermath of the First World War, a sufficiently large number of European entomologists would be able or be enabled to bear the expenses of a visit to the United States. However the optimistic view was eventually taken and proved to be justified, since the Carnegie Endowment for International Peace gave a grant of $5,000 toward the cost of transportation of European entomologists and the organizing committee succeeded in getting support from many sides and in collecting a considerable sum of money to pay for the entertainment of the guests from Europe and other foreign countries. The Congress was actually held at Cornell University in Ithaca, New York and had a registered membership of 717 of whom 611 actually attended. Of these the great majority were entomologists from the United States and Canada but there was a reasonably good representation from overseas and a sufficient number of contributions from foreign delegates to maintain the international character of the Congress. Dr. L. O. Howard presided over this Congress with Professor W. M. Wheeler and Professor James G. Needham as

Vice-Presidents and Professor O. A. Johannsen as General Secretary. At this Congress Professor O. A. Johannsen was elected a member of the Executive Committee to replace Dr. H. Skinner who had died in the interim period, and Dr. W. J. Holland and Professor S. A. Forbes were made Honorary Members. The Ithaca Congress was very successful. Its most striking feature was perhaps the predominance of papers relating to economic entomology, but the scientific aspects of the subject were also dealt with in many interesting papers.

In 1932 the Entomological Society of France celebrated its centenary. The Executive Committee of the Congresses therefore considered it desirable to hold the Fifth International Congress of Entomology on that occasion. The Congress was held in the Lecture rooms of the Institut National Agronomique under the Presidency of Professor Paul Marchal with P. de Peyerimhoff, Etienne Rabaud and J. Villeneuve de Janti as Vice-Presidents, the General Secretary being Professor R. Jeannel. Over 250 entomologists attended this Congress and there was over a score of representatives from Canada and the United States. On this occasion the French Government paid the travelling expenses of twelve entomologists from various foreign countries and contributed to the expenses of another fourteen members representing France and neighbouring countries. By the date of this Congress only nine Honorary Members had survived; of these Professor Horvath, Professor Matsumura and Professor Poulton attended the Congress. Professor E. L. Bouvier, Dr. L. O. Howard, Professor A. Lameere and Dr. A. Von Schulthess were proposed as new Honorary Members and accepted by the Congress.

The Executive Committee announced that it had received three invitations to the next Congress: one from the King of Egypt, one from Germany and one from Spain. Since the International Congress of Zoology was to be held in Lisbon in 1935 the Executive Committee decided to recommend the holding of the Sixth Congress in that year in Madrid. This proposal was accepted and Professor I. Bolivar y Urrutia was elected President. This appears to have been a very successful Congress with representatives from many parts of the world. However the published Proceedings at my disposal do not contain an account of the business meetings with the resolutions and the decisions of the Executive Committee. In fact before the Congress paper could be published Civil war broke out in Spain and this did not end officially until March 29th, 1939. The papers presented at the Congress were not published until 1940.

However at the Madrid Congress it was decided that the Seventh Congress should be held in Berlin. Professor E. Martini was elected President of the Congress with Dr. M. Schwartz as Vice-President and Dr. E. M. Hering as the General Secretary. This was in point of numbers by far the most important Congress held up to that time. The registered membership was 1151 of which 936 actually attended and 60 countries were represented. There was of course an extremely large representation from Germany itself. We may note as a matter of historical interest that General Goering and Count Von Ribbentrop were members of the Honorary Committee. The Programme was extensive and well organized containing much interesting material but it was held in an atmosphere of tension and marred by extreme nationalist manifestations by representatives of certain countries. From then onward there followed rapidly the series of events which led to the Second Great War. One would prefer to forget the expressions of aggressive nationalism that led up to the catastrophe were it for the fact that some of the most respected members of the entomological corporation followed the party line with fervent and undisguised enthusiasm.

The Executive Committee after the Berlin Meeting decided that the Eighth Congress should meet at Stockholm in 1941 and the Ninth Congress in Holland in 1945 on the occasion of the Centenary of the Dutch Entomological Society. In view of the prevailing atmosphere at the time, this proposal seems unduly optimistic, to say the least. In fact, twelve years elapsed before it again became possible to hold an International Congress of Entomology. Nevertheless the plans made before the outbreak of the Second Great War were eventually carried out. The Eighth Congress actually met in the summer of 1950 in Stockholm under the Presidency of Professor Ivor O. H. Tragårdh with Dr. C. Olov Lundblad as Vice-President and Professor Victor Butovitsch as General Secretary. It opened with an excursion on August 7th and terminated with a series of other excursions of which the last took place on August 19th. The week of August 9th to 14th was occupied by the scientific and business sessions. This Congress was extremely successful. I have not been able to calculate the attendance from the information at my disposal but it appears to have been larger than that of any preceding Congress except perhaps the one held in Berlin. An interesting collection of scientific papers was presented and many of these were of a high level, clearly indicating the great scientific development of entomology during the forty years that had elapsed since the First Congress. At this congress a number of important decisions were taken. Dr. Karl Jordan who had been Permanent Secretary of the Executive Committee since the foundation of the Congresses resigned his position and was elected Honorary Vice-President of the Congress and Honorary Life Member of the Committee. Dr. O. A. Johannsen of the United States, Dr. MacGillivry of Holland, Dr. Karl Holdhaus of Austria and Dr. A. D. Imms of Great Britain were elected Honorary Life Members. At the request of the International Union of Biological Sciences which is a division of UNESCO (United Nations Educational, Scientific and Cultural Organization) the Congress agreed that the Executive Committee should become a section of the International Union of Biological Sciences. Finally the Executive Committee recommended that Mr. N. D. Riley, Keeper of Entomology in the British Museum be elected to the post of Secretary to the Executive Committee rendered vacant through the retirement of Dr. Jordan and automatically to the secretaryship of the Entomological section of the International Union of Biological Sciences. The financial support obtained from UNESCO through the intermediary of the International Union of Biological Sciences for our Congress in Montreal indicates that the decision will have results beneficial to the congresses. It was then recommended that the next congress be held in 1951 in Holland.

The Ninth Congress was therefore held in August 1951 in Amsterdam under the Patronage of Her Majesty Queen Juliana. It had a registration of almost one thousand members, including representatives from several distant countries. Five Canadian and eight American entomologists attended. This Congress was also characterized by the high quality of the scientific contributions. It was held under the Presidency of Dr. D. J. Kuenen of Leyden with Professor L. F. de Beaufort as Vice-President and Dr. J. de Wilde as Secretary. At this Congress it was decided that the body hitherto known as the Executive Committee be known henceforth as the Permanent Committee, that in future no life subscriptions of any kind be accepted and that all institutional life subscriptions be terminated forthwith. At the conclusion of this Congress the Permanent Committee was made up of the following members. Dr. H. E. K. Jordan, Honorary Life Member; Dr. R. Jeannel, President; Mr. N. D. Riley, Secretary with Dr. C. Bolivar y Pieltain, Dr. J. Chester Bradley, Dr. E. M. Hering, Dr. D. J. Kuenen,

Dr. M. N. Rimsky-Korsakoff and Dr. T. Shiraki as members. The name of Dr. R. Jeannel was added to the list of Honorary Members.

In the closing section of the Ninth Congress the Secretary of the Permanent Committee announced that though no decision had yet been taken as to the site of the next Congress it was hoped to hold it in 1955 and he revealed that of several invitations received the most attractive had come from the Government of Brazil. The Brazilian entomologists indeed made plans to hold the Congress in that country but unforeseen difficulties made this impossible and eventually at a date which was very late, having regard to the difficulties of organizing the large International Congresses that have now become customary, the Entomological Society of Canada, at the pressing request of the Permanent Committee, agreed that the Congress should be held in Canada. The site chosen by the Canadian Executive Committee was the City of Montreal, because it is the largest and most cosmopolitan city of Canada, in many ways the most representative of the national character, and the one which most nearly resembles the great European centres in which the Entomological Congresses have been held in the past. We hope that the members now assembled will feel at the conclusion of the Congress that the choice of Canada has been justified by the character of the Congress.

As the Prime Minister of Sweden pointed out in opening the Stockholm meeting "an International Scientific Congress, has, besides the professional exchange between colleagues an essential importance in so far as it is a manifestation of scholarly and scientific internationalism". This apparently axiomatic statement, he said, need not have been made had it not been that this very generation has experienced frightening attempts to vindicate an opposite opinion so that all are now aware that they have to be on their guard against tendencies to enslave scholarly research to nationalistic or imperialistic interests. Dr. Karl Jordan speaking at the same meeting drew consolation from the fact that on some points relating to biological nomenclature scientists have been able to agree and he concluded from this that they will eventually agree on others which are equally rational and desirable, and expressed the hope that little by little they would reach a general agreement on matters that deeply affect the welfare of mankind. Certainly we will all share the hope of the revered Father of the International Congresses of Entomology; but after the bitter experience of the past years we may wonder, considering how we have come to our present pass, whether the results of biological research, as they are interpreted by many of its modern representatives, will give men of science the fortitude to resist the encroachments of a materialistic state and provide them with the moral principles on which international harmony can arise. All realize that while we appear to be faced with the alternative described in Wendell Wilkie's lapidary phrase: *one world or none*, it is possible to conceive of a world that is a unit, yet dominated by a spirit alien to the development of science. At all events, we may hope that the friendships made in this Canadian Congress will help to dissipate the misunderstandings that isolation engenders and help the world to advance even if only a small step toward the ideal of peace with justice to which we all aspire.

Entomology in Canada up to 1956

A Review of Developments and Accomplishments

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1 Chief of Division.

Introduction

Entomology in Canada began about the middle of the nineteenth century with a small but able group of hobbyists. They became active shortly before confederation in what was then the Province of Canada, a temporary union of the present provinces of Ontario and Quebec. Today, a century later, the science is firmly founded throughout the country with over 400 professional entomologists, more than 50 well-equipped research centres, 16 institutions giving formal instruction, and eight professional societies. Entomological advisory services are established in several provinces and federal legislation protects the public against the spread of noxious insects and the fraudulent or dangerous sale of materials for their control.

Many factors have contributed to this development, but the underlying and recurring stimulus has been the economic necessity imposed by the insects themselves. Thus, entomology in Canada has developed largely as an applied science with the Canada Department of Agriculture playing a leading role. Fortunately, the basic and theoretical aspects have also received attention, first in the colleges and universities and later in the modern government laboratories. The course of events has been profoundly influenced by outstanding leaders—Bethune, Saunders, Fletcher, Lochhead, Hewitt—during the critical, formative years; by the immense contribution, both practical and professional, of the Entomological Society of Ontario and its branches; by the early establishment of centres for entomological instruction; by the effective support of the agricultural and forest industries and their associated organizations; by our proximity to the United States from which immeasurable benefits have derived; and finally, by the economic boom that swept Canada and the Western World in the wake of the Second World War.

A complete account of developments and accomplishments is beyond the scope of this paper. Indeed, it was necessary to leave out more than has been included. In the plan adopted, a historical review is followed by summary accounts of selected fields of work. Each section has been prepared by an appropriate Canadian authority with wide latitude for both content and treatment. The resulting lack of uniformity is, admittedly, a defect, but we trust a minor one where the primary purpose is to present a synoptic picture of the rise and progress of entomology in Canada.

For further details the reader is referred to the following review articles: on the period up to 1898, C. J. S. Bethune[2]; on applied entomology in Canada before 1915, C. G. Hewitt[3], and between 1914 and 1923, A. Gibson[4]; on applied entomology in Ontario before 1903, W. Lochhead[5], and between 1863 and 1938, L.

2 Trans. Roy. Soc. Canada, 2nd Ser., 4 (Sec. 4): 155-165, 1898.
3 45th Ann. Rept. Ent. Soc. Ont. (1914): 29-41, 1915.
4 16th Ann. Rept. Que. Soc. Prot. Plants (1923-24): 24-56, 1924.
5 34th Ann. Rept. Ent. Soc. Ont. (1903): 22-26, 1904.

Caesar;[6] on general developments in Nova Scotia up to 1938, A. D. Pickett and H. G. Payne,[7] in Quebec up to 1939, G. Maheux,[8] and in British Columbia up to 1951, various writers;[9] and on the federal entomological service between 1887 and 1937, A. Gibson.[10] In addition, the well-documented manuscript "Entomology in Canada", by A. Gibson, covering in detail the period up to 1944, is filed in the Entomology Division Library, Ottawa.

The physiography, climate, soils, and vegetation of Canada are described by E. G. Munroe[11] in a companion paper in this issue.

Historical Review

The history of entomology in Canada is an integral part of the broader story of land settlement and the development of our natural resources. Three broad stages of development are discernible: the long period of entomological awakening and the rise of professionalism (up to 1909); the determinative period (1910 to 1945), when the national and provincial services took shape; and the period of expansion and reorientation that began with the close of the Second World War and is still in course.

The Beginnings: Before 1910

The beautiful butterflies, the tormenting mosquitoes, and the devastating locusts drew repeated notice in the early Canadian records; an experiment with bees was conducted in 1749; and caterpillars attacking apple trees gave rise to preventive legislation in the Parish of Montreal as early as 1805. Nevertheless, prior to the 1850's entomology consisted solely of the hobby interests of a few individuals scattered through the settled areas of Upper and Lower Canada. Most of the country was still a wilderness although agriculture and lumbering were already thriving and featured the export of wheat and white pine. There were no named insect reference collections and the links with the established entomological world were confined to overseas correspondence, aid from friendly contemporaries in the United States, and a few important books, of which only those written by the Rev. William Kirby[12] and by P. H. Gosse[13] contained information about species then known to occur in this vast new land.

In the beginning, outlets for publication were few, but great encouragement resulted from the founding of two periodicals in which the early entomological literature, predominantly descriptive, became concentrated: *The Canadian Journal* (Toronto, 1852) and *The Canadian Naturalist and Geologist* (Montreal, 1856). Among the important early contributors were William Couper, Thomas Cottle, W. S. M. D'Urban, William Saunders, and C. J. S. Bethune, who in 1862 presented his famous "List of Entomologists in Canada"[14]—the names of 36 persons interested in collecting and studying insects.

In the first half of the century serious losses to the wheat crops occurred periodically from the hessian fly, *Phytophaga destructor* (Say), the wheat midge, *Sitodiplosis mosellana* (Gehin), and other noxious forms. The situation became alarming in 1856 with destruction estimated in excess of two million dollars in Canada West[15] (Ontario) alone. The Bureau of Agriculture and Statistics of the then Province of Canada, in desperation, offered prizes for the three best essays on the subject. First prize (£40) was won by H. Y. Hind, Professor of

6 69th Ann. Rept. Ent. Soc. Ont. (1938): 7-10, 1938.
7 69th Ann. Rept. Ent. Soc. Ont. (1938): 11-15, 1938.
8 70th Ann. Rept. Ent. Soc. Ont. (1939): 7-14, 1939.
9 Proc. Ent. Soc. B.C. 4: 39-44, 67-71, 1914; 13: 135-146, 1921; 48: 9-36, 1952.
10 Proc. 7th Int. Cong. Ent. (Berlin, 1937) 3: 1429-1479, 1939.
11 *Canadian Ent.* 88: 372-476, 1956.
12 Fauna Boreali-Americana, Part 4. Josiah Fletcher, Norwich. 1837. (Included descriptions of 447 species of insects collected during the Second Franklin Expedition of 1825).
13 *The Canadian Naturalist.* John van Voorst, London. 1840.
14 *Canadian Nat. Geol.* 7: 199-201, 1862.
15 Trans. Roy. Soc. Canada, 2nd Ser., 4 (Sec. 4): 158, 1898.

Chemistry at Trinity College, Toronto, for his "Essay on the Insects and Diseases Injurious to the Wheat Crops", which was printed and distributed to farmers in 1857. This action marks the first entomological service sponsored by a government in Canada. Also in 1857, l'Abbé Léon Provancher listed eight pest species attacking wheat crops in Canada East (Quebec)[16]. With these two articles our economic literature began.

By this time interest in entomology was rising rapidly. On September 26, 1862, the Rev. C. J. S. Bethune, an Anglican clergyman who later (1907) became Head of the Department of Entomology and Zoology at the Ontario Agricultural College, and William Saunders, a druggist in London, Canada West, who later (1896) became the first Director of the Dominion Experimental Farms Branch, arranged the first meeting of entomologists ever held in Canada. At the home of Prof. Henry H. Croft (University of Toronto) 10 persons met to form an entomological society and draft its objectives. However, the actual organization was postponed until April 16, 1863, when the Entomological Society of Canada came into being with headquarters at Toronto, Croft as President, Saunders as Secretary-Treasurer, the Rev. J. Hubbert as Curator, and a membership of 25.

The formation of this society led immediately to an increase in the number of articles describing the appearance and habits of insects. This, in turn, encouraged the Society in 1868 to establish its own journal, *The Canadian Entomologist.* Systematic entomology received a further impetus when Léon Provancher, the father of natural history in Lower Canada, turned his talents and great energy in this direction. Between 1877 and 1890 his *Petite Faune entomologique du Canada* appeared in three volumes plus several supplements and totalled nearly 3,000 pages. In 1868 he founded the periodical *Le Naturaliste Canadien* and remained its editor and chief contributor until his death in 1892.

Meanwhile, insect pest problems grew steadily worse and in 1869 the Board of the Agricultural and Arts Association of Ontario—the provincial agricultural association of the day—voted $400 to the Society for the year 1870 on condition that it furnish an annual report on noxious insects, provide the Association with a cabinet of insects, and continue to publish its journal. These conditions were accepted and the Annual Report for 1870, featuring insects affecting the apple, the grape, and the plum, and published in 1871, became the first of a continuing series. The Government of Ontario likewise turned again to the Society, first in reference to the dread Colorado potato beetle, which had invaded the province in 1868, and later on a more permanent basis. In return for an annual government grant and an offer to publish the Annual Report, the Society agreed to become incorporated in 1871 as the Entomological Society of Ontario.

Fortunately for Canada many of the pioneer naturalists were exceedingly able men. Their outstanding articles soon made the annual reports of the Society an invaluable source of practical information for the farmer, orchardist, and gardener of early Canada. It was also fortunate for entomology in general that the Ontario society continued to function essentially as a national organization with which affiliated branches were eventually formed in several other provinces. A national viewpoint in entomology was thus preserved until the Entomological Society of Canada was re-established in 1950. A short history and related articles were published in *The Canadian Entomologist* for January, 1939, to commemorate the 75th anniversary of the founding of the Entomological Society of Ontario.

The year 1883 was made memorable by two events: the publication of Saunders' remarkable book, *Insects Injurious to Fruits*[17], which remained the

16 Essai sur les insectes et les maladies qui effectant le blé. Presses à vapeur du Canada Directory, rue St. Nicholas, Montreal. 1857.

17 J. B. Lippincott Co., Philadelphia, 1883.

principal North American reference in this field for several decades; and the appointment of James Fletcher, a distinguished naturalist, as Honorary Entomologist to the Dominion Department of Agriculture. The following year, Fletcher was appointed Dominion Entomologist, but he also continued his duties as accountant in the Library of Parliament. However, in 1887, following the establishment of the Experimental Farms Branch (1886), he was transferred from his parliamentary post and became Dominion Entomologist and Botanist, a position he filled with distinction until his death in 1908. Although he never had more than two assistants he established a remarkable correspondence with farmers throughout Canada, his 400 regular observers forming an effective insect reporting service. By this means he "surveyed" distant areas, built up a useful reference collection, kept himself informed on the pest situations that arose as the West and other regions were opened to settlement, and dispensed advice and encouragement. He was also responsible for the San José Scale Act of 1898, the first federal legislation on noxious insects; and his 24 annual reports provide a monumental record of our developing economic entomology.

In the meantime other significant developments had occurred. Several provinces had passed legislation concerning noxious insects; for example, against the Colorado potato beetle in Prince Edward Island in 1883, against the San Jose scale in Ontario and in Nova Scotia in 1898, and to provide for an inspector of insect pests in British Columbia in 1892. Vigorous affiliated branches of the Entomological Society of Ontario had flourished in Montreal, Que., since 1873, and in British Columbia since 1902; and, through the leadership of Prof. William Lochhead, the Quebec Society for the Protection of Plants, with its own published annual reports, was established in 1908 in Quebec City. A. W. Baker[18] reports that instruction, leading to special training in entomology, was begun at the Ontario Agricultural College in 1877 under Peter H. Bryce and in Quebec at Macdonald College in 1907 under Lochhead, assisted by J. M. Swaine; apiculture was taught at O.A.C. prior to 1895; a course in forest entomology was added at the University of Toronto in 1908 with E. M. Walker in charge; and lectures in entomology were included with the regular instruction at the School of Agriculture, Truro, N.S., beginning in 1888, and at the Manitoba Agricultural College in 1906. Simple experimentation had led to the common use in Eastern Canada and to a considerable extent in British Columbia of insecticides such as paris green, kerosene emulsion, lime-sulphur, and tobacco extract. Strong ties had been forged between entomologists in Canada and the United States, as evidenced by the formation in 1889 of the American Association of Economic Entomologists, which resulted from a meeting held in Toronto under the joint sponsorship of Fletcher and his American counterpart and friend, L. O. Howard. Finally, the scientific achievements of such entomological leaders as Saunders, Bethune, Provancher, Fletcher, and the Rev. G. W. Taylor of British Columbia had been fittingly recognized by their election to fellowship in the Royal Society of Canada.

Thus by the early 1900's entomology was firmly established as an important science and as an essential service. The final step in the rise of professionalism was the separation of entomology and botany into distinct divisions of the Experimental Farms Branch and the appointment in 1909 of Dr. Charles Gordon Hewitt, a fully trained scientist from England, to succeed Fletcher as Dominion Entomologist.

18 60th Ann. Rept. Ent. Soc. Ont. (1929): 33-46, 1929.

The Middle Years: 1910-1945

The Canada of 1910 was vastly different from that of the 1850's. It was united politically since the passage of the British North America Act of 1867 and geographically since the completion of the trans-Canada railroad in 1885; provincial territories were defined throughout the prairie region and settlement there was booming; and education, a provincial responsibility, had kept pace through the establishment of colleges or universities in every province. The events of the past half century signified more clearly than ever that Canada's future lay in her great potential to produce food and fibre; and the importance of insect pest control to such production had already been amply demonstrated. But the nation's entomological resources were woefully inadequate. The time for expansion of entomological services was at hand and leadership was of paramount importance.

Hewitt was at once a dominant influence. Under his leadership the important Destructive Insect and Pest Act was passed in 1910. The Act and the Regulations subsequently approved by Order-in-Council under the Act still form the legal basis for national action against the introduction and spread of noxious insects in Canada. But perhaps of equal historical importance is the fact that the administration of the Act required more funds and staff than had been made available hitherto for entomological work. Thus, until the fiscal year 1934-1935, the funds obtained under the authority of the Insect Section of the Act provided the principal support for federal entomology and the sole support for the field laboratories. Thereafter, such funds were included in the regular Entomology Vote. Between 1911 and 1919 Hewitt established small laboratories in all provinces except Prince Edward Island; and in 1912 he appointed J. M. Swaine as his assistant in charge of forest entomology, a field of work hitherto neglected. In 1914, federal responsibility in insect control was further recognized by separating entomology from the Experimental Farms Branch and establishing a distinct Entomological Branch of the Department. The Branch was soon organized into four functional divisions: Field Crop and Garden Insects (1914), Forest Insects (1914), Foreign Pests Suppression (1919), and Systematic Entomology (1919). This foundation laid by Hewitt was accepted, although subsequently expanded and modified, by his successors: Arthur Gibson (1920-1942), L. S. McLaine (1942-1943), H. G. Crawford (1943-1950), and Robert Glen (1950-).

The passage of the Destructive Insect and Pest Act and the developments that followed stimulated related activities in the provinces. Comprehensive protective legislation was introduced in 1911 in Nova Scotia, in 1913 in New Brunswick, and in 1914 in Quebec; provincial entomologists were appointed in 1912 in Ontario (L. Caesar), British Columbia (W. H. Brittain), and Nova Scotia (Robert Matheson), in 1913 in Quebec (Canon V. A. Huard), and somewhat later in New Brunswick (W. McIntosh); additions were made to the entomological teaching staffs at several agricultural colleges; a few provincial laboratories and fumigation stations were established to work in close collaboration with their federal counterparts; and facilities for communicating entomological information were improved through the founding in 1911 of the *Proceedings of the Entomological Society of British Columbia*. However, the advent of the First World War temporarily halted such developments.

In the period between 1918 and the close of the Second World War in 1945, Canada's farming and forest industries spread and matured. Likewise, the threat from insects increased. Grasshoppers, cutworms, wireworms, and the wheat stem sawfly took repeated heavy toll from the grain crops in the Prairie Provinces; serious infestations developed in stored grain, especially under war-time storage

conditions; warble flies and the horn fly continued to plague livestock; orchards were threatened with disaster from the codling moth; and forests faced further ravages from the spruce budworm, the European spruce sawfly, the hemlock looper, and various species of bark beetles. The seriousness of the situation was increased and the financial support temporarily withered by the widespread economic depression of the 1930's. Nevertheless, during this quarter century entomology continued to make slow but steady progress under the influence of Gibson, McLaine, Swaine, Treherne, and deGryse of the federal department, Caesar (Ont.), Maheux (Que.), and Brittain (N.S.), of the provincial services, and Walker (Toronto), Baker (O.A.C.), DuPorte (Macdonald), Strickland (Alberta), and Spencer (British Columbia) in the colleges and universities.

The organization of the Entomological Branch was altered in 1932 with the appointment of H. E. Gray as officer-in-charge of stored product insect investigations and in 1938 with the formation of the Fruit Insect Investigations Unit under W. A. Ross.

Federal laboratories and staffs were gradually increased, the most notable new building being the quarantine laboratory at Belleville (1936) with its special facilities for the propagation of imported parasites and predators. The Forest Insect Laboratory at Sault Ste. Marie, built in 1944 by the Ontario Department of Lands and Forests and staffed and equipped by the Canada Department of Agriculture, was another valuable addition. However, these were striking exceptions to the generally inadequate federal buildings and laboratory facilities that persisted in the wake of depression and war and an applied entomology founded almost exclusively on field projects. Instruction in entomology became available at eight additional centres and the subject was further recognized through the establishment of special options at the Ontario Agriculture College (1920) and Macdonald College (1920) and of separate departments of entomology at the latter (1921), the University of Alberta (1922), and the University of Montreal (1931). Provincial spray services were developed, notably by the departments of agriculture in Ontario, Nova Scotia, and Quebec; the Quebec Department of Lands and Forests established an entomological service; and a provincial entomologist was appointed in Manitoba. Legislation was passed by the provinces of Alberta and Manitoba against insect pests in general, by Saskatchewan in relation to grasshopper control, and by the federal department concerning the registration and sale of pesticides. In 1921, the International Great Plains Conference of Entomologists was formed in the interests of both American and Canadian workers in that region; and the Nova Scotia Branch of the Entomological Society of Ontario widened its coverage, was renamed the Acadian Entomological Society, and received financial support from the provinces of Nova Scotia and New Brunswick until it became temporarily inactive about 1925. A useful college reference was provided by W. Lochhead's *Class Book of Economic Entomology*[19]; and new outlets for scientific papers were added by the founding of three important periodicals: *Scientific Agriculture*[20] (1921), *The Forestry Chronicle*[21] (1925), and *Canadian Journal of Research*[22] (1929). Improved recording of seasonal developments in the insect pest situation was undertaken by the Entomological Branch through *The Canadian Insect Pest Review*, a comprehensive

19 Blakiston's Son and Co., Philadelphia, 1919.

20 Scientific journal of the Agricultural Institute of Canada; since 1953, named Canadian Journal of Agricultural Science. Published by the Queen's Printer, Ottawa, under the authority of the Chairman of the National Committee on Agricultural Science.

21 The official journal of the Canadian Institute of Forestry, Toronto.

22 Published by the National Research Council of Canada, Ottawa, under tht authority of the Chairman of the Committee of the Privy Council on Scientific and Industrial Research. From 1935 to 1951 the zoological articles were published separately as Section D and since 1951 as a distinct periodical, *Canadian Journal of Zoology*.

mimeographed publication issued several times yearly beginning in 1923, and its detailed *Annual Report of the Forest Insect Survey*, starting in 1936.

Perhaps the most significant event of the period was the reorganization of the Canada Department of Agriculture in 1937. By this action, Science Service was created as the main scientific arm of the Department, with five research divisions: Entomology, Botany and Plant Pathology, Animal Pathology, Chemistry, and Bacteriology and Dairy Research. The former Entomological Branch thus became the Entomology Division of Science Service and the former Division of Foreign Pests Suppression was divorced from Entomology and included in a separate Plant Protection Division, with L. S. McLaine in charge, and transferred to Production Service, from which it returned in 1942 as the sole regulatory division in Science Service. J. M. Swaine directed the new Service until his retirement in 1945.

During the Second World War excellent contributions were made by Canadian entomologists to the protection of vital crops and materials and to the welfare and comfort of the armed forces. But entomology as a science stood still. Thus the second era in Canadian entomology closed quietly with the federal department firmly established in applied research, with some 140 full-time entomologists, the provincial departments, universities, and colleges taking greater leadership in advisory services in most fields, and all groups working closely in an effective informal collaboration.

The Recent Period: 1945-1956

The cessation of hostilities in 1945 introduced a period of unprecedented economic and scientific prosperity. The first entomological implication arose from the return to university of large numbers of war veterans, many to procure training in and subsequently to seek jobs in entomology, for which the Canada Department of Agriculture was already the principal employer. This enormous and sudden increase in enrolment at colleges and universities so completely occupied the available facilities and staffs in teaching that comparable attention to research at these centres had to be delayed. These developments coincided with increased financial support for entomological research, especially from federal sources. Consequently, the post-war period was not only characterized by advances in all aspects of entomology but particularly by unprecedented expansion in the federal service, notably in forest entomology.

After a lapse of nearly 80 years, the Entomological Society of Canada was reinstated on November 3, 1950; and in 1956 it was incorporated under the Canada Companies Act. At present there are seven regional societies: the entomological societies of Ontario (1871), British Columbia (1902), Manitoba (1945), Quebec (1951), Alberta (1952), and Saskatchewan (1953), and the Acadian Entomological Society, which serves the four Atlantic provinces and which emerged in 1949 from a rather protracted diapause. In 1951, the Montreal Branch, the oldest branch (1873) of the Entomological Society of Ontario, became the Montreal Section of the Entomological Society of Quebec. The regional societies are autonomous, some being incorporated under provincial statutes, but all are affiliated with the national organization. Thus the Entomological Society of Canada is the one body that represents Canadian entomologists as a whole. Beginning in January, 1951, *The Canadian Entomologist* was published jointly by the national society and the Entomological Society of Ontario; and subsequently assistance in publication was received through other regional societies. A new outlet for works of monographic scope was provided in 1955 by the inauguration of supplements to *The Canadian Entomologist*. However, perhaps the major

decision taken by the national society since its rebirth was the sponsorship of the Tenth International Congress of Entomology, which will be held in Montreal in August, 1956, and will add still another highlight to the entomological history of this country.

The principal change in entomological instruction was at the advanced post-graduate level. At the end of the Second World War only the University of Toronto and McGill University (Macdonald College) conferred the Ph.D. degree with a major in entomology. Today it is granted by seven additional institutions: University of Western Ontario, Queen's University, University of Manitoba, University of Saskatchewan, University of British Columbia, Laval University, and the University of Montreal. However, none of these graduate schools is large by North American standards and many Canadian students seeking their doctorate still prefer to attend one of the several highly developed centres in the United States. Students proceeding to advanced work may be assisted financially through the educational leave policy of the Canada Department of Agriculture or through scholarships provided by the National Research Council, the Agricultural Institute of Canada, provincial government departments, provincal research councils and foundations, and certain industries. To summarize: formal instruction in entomology is now procurable in all provinces except Prince Edward Island and Newfoundland; from 30 to 35 staff members at some 16 colleges and universities include the teaching of entomology among their major responsibilities; the M.Sc. degree in entomology is offered in a dozen institutions, the Ph.D. in nine; the Ontario Agricultural College, the oldest centre of instruction, still has the largest teaching staff; and Macdonald College still remains the principal graduate school.

In British Columbia, an able corps of extension horticulturists has borne much of the advisory load in recent years; and in the other mainland provinces, especially in Ontario and Quebec, provincial district officers and college staffs have gradually assumed greater responsibility for entomological extension in the agricultural field. These and earlier developments have shifted to the provinces much of the responsibility for protective services and for organizing large-scale pest control campaigns. Nevertheless, provincial officers are unable as yet to carry the full advisory burden in the field of agriculture and public health and many federal entomologists still act as extension specialistis in the areas served by their laboratories. In forest entomology, consultative and advisory work has continued primarily as a federal function.

Legislation concerning pest control kept pace in provincial, national, and international circles. For example, the Warble Fly Control Act was passed in Ontario in 1952 and amended in 1953 and 1955; all existing Regulations of the Destructive Insect and Pest Act (1910) were revoked and re-established in consolidated form in 1949 and again in 1954; registrations of insecticides under the Pest Control Products Act (1939) trebled in number between 1945 and 1955; and in 1951 Canada joined some 27 other countries in signing the International Plant Protection Convention, which is administered by the Food and Agriculture Organization of the United Nations.

Entomological research more than doubled in volume in the decade following the Second World War. This remarkable increase occurred largely in the Canada Department of Agriculture, which in 1956 employed over 350 full-time professional entomologists[23] and conducted at least 85 per cent of the entomological investigations in Canada. Virtually all of this expansion related directly

23 Listed in A Directory of Canadian Entomologists, published by the Tenth International Congress of Entomology, Ottawa, 1956.

or indirectly to pest problems. Nevertheless, the period marked the rise and establishment in Canada of basic work in insect physiology, toxicology, pathology, genetics, and cytology; and important developments in theory and concept in related fields such as insect behaviour, population dynamics, and systematics. The first intensive exploration of the insect fauna and the biting fly problem of arctic and sub-arctic Canada was begun in 1947 as a joint undertaking between the Entomology Division and the Defence Research Board of the Department of National Defence. The Board contributed funds, transport, and the special facilities and assistance of its entomology sections (since closed) at Suffield, Alta., and Churchill, Man. Co-ordination was achieved through the Entomological Research Panel, an advisory body established by the Board in 1947 with membership from universities and appropriate federal departments.

Dynamic leadership in Science Service[24] was a major contributing factor to the post-war growth and improvement in federal research. In 10 years the status of the investigator has been vastly bettered in terms of relative salary, prestige, opportunity for travel, and working conditions; large modern laboratories have been built at some 15 centres; headerhouses, greenhouses, insectaries, etc., have been added at a dozen other locations; all essential facilities and conveniences have been provided, including comprehensive reference libraries, a variety of transport, and land for experimental purposes; co-operation with other research institutions has been broadened through the establishment of federal research grants for work on Science Service projects; and, by arrangement with the National Research Council, a number of post-doctorate fellowships are now tenable at Science Service laboratories.

Many of the new laboratories are designed to bring together scientists from the different research divisions in the Service to permit teamwork under unified direction; and administration is being consolidated and re-channelled in an effort to reduce the routine activities that hitherto have burdened officers directing research. In achieving these changes, entomology has been placed in a more intimate working relationship with other agricultural sciences, but it is gradually surrendering much of its former autonomy in the interests of the larger, integrated organization.

During the post-war period several important changes affecting entomology have been made in the organization of the Canada Department of Agriculture. In the Entomology Division, the Biological Control Unit was formed in 1948 and in 1955 it was combined with the Systematic Entomology Unit into the Insect Systematics and Biological Control Unit; also in 1948 Stored Product Insect Investigations, Livestock Insect Investigations, and Household and Medical Entomology were raised to unit status, the last two being combined in 1952 into the Veterinary and Medical Entomology Unit. In 1951, the Forest Biology Division was created in Science Service and the Forest Insect Investigations Unit was transferred to it from the Entomology Division; and in 1956, the Plant Protection Division was transferred from Science Service to the Production Service of the Department. The services, divisions, and units (shown in parentheses) currently concerned with entomology are as follows: In Science Service, the Entomology Division with five units (Insect Systematics and Biological Control, Field Crop Insects, Fruit Insects, Stored Product Insects, and Veterinary and Medical Entomology) and the Forest Biology Division (Forest Zoology); in Production Service, the Plant Products Division with two units concerned with pesticides

24 Senior officers in Science Service work together as an Executive Committee but those in positions of greatest influence on entomology in the period under review included the Director (K. W. Neatby, 1946-); Associate Director (W. E. van Steenburgh, 1947-); Chief, Entomology Division (H. G. Crawford, 1943-1950; R. Glen, 1950-); Chief, Forest Biology Division (J. J. de Gryse, 1951-1952; M. L. Prebble, 1952-); and Chief, Plant Protection Division (W. N. Keenan, 1942-).

(Inspection Services and Laboratory Services) and the Plant Protection Division (Plant Inspection Service); and in Experimental Farms Service, the Apiculture Division.

Canadians might well take satisfaction from the progress attained in the first one hundred years of entomology. But there is no cause for complacency. Most of Canada still remains to be surveyed intensively for its insects; merely a beginning has been made on the perplexing problem of the mechanisms that affect the abundance of a species; the costs of control and the toxic residues on produce and in soils require continued attention; and many new entomological fronts will arise from such prospective developments as settlement of the northland, widespread industrial growth, enlargement of universities, and shifting emphases in agriculture and forestry. Fortunately, entomology in Canada is in a relatively strong position to meet the challenge of its second century.

Systematic Entomology

A distinction must be made between the history of the systematics of Canadian insects and the history of systematic entomology in Canada. The earliest contributions to the systematics of Canadian insects were made not by Canadians, or in Canada, but by foreign systematists such as Kirby, Curtis, and Walker of England, LeConte, Horn, Osten Sacken, Cresson, and Edwards of the United States, and many others from these and other countries. The material on which these pioneers based their studies was obtained on collecting or exploring expeditions to Canada (such as the Second Franklin Expedition in 1825), from paid collectors resident in Canada, or from some of the early Canadian amateur entomologists, who submitted specimens to foreign specialists for determination and description. Foreign systematists continue to make contributions to the knowledge of the Canadian fauna although their output in this direction is now overshadowed by that of resident Canadian systematists, who in turn have worked extensively on the fauna of North America and to some degree on that of other countries.

The history of systematic entomology within Canada commenced with l'Abbé Léon Provancher of Quebec, who in the 1870's made substantial and noteworthy contributions to the knowledge of Canadian Coleoptera, Hymenoptera, and Hemiptera, his most important work being the *Petite Faune entomologique du Canada* (1877-1886). About Provancher's time, and in the decades following, there were a number of important amateur collectors in Canada, some of whom published fairly extensively. Today there are, unfortunately, rather few active amateur systematists in this country, and most of those that remain are of the senior generation. Of the more notable amateurs, past or present, mention may be made of W. Couper, N. Criddle, J. D. Evans, E. R. Buckell, G. Chagnon, and Brother A. Robert, who collected and studied insects of several orders; W. H. Harrington, F. W. L. Sladen, G. W. Taylor, and J. A. Guignard, whose main interests and contributions were in the Hymenoptera; J. F. Hausen, H. B. Leech, J. B. Wallis, and G. Stace Smith (Coleoptera); W. S. M. D'Urban, H. H. Lyman, A. F. Winn, C. J. S. Bethune, C. H. Young, A. Gibson, G. S. Brooks, A. C. Sheppard, F. H. Wolley-Dod, K. Bowman, C. H. Blackmore, and J. R. J. Llewellyn-Jones (mainly Lepidoptera); C. B. D. Garrett and Brother J. Ouellet (Diptera); G. A. Moore, J. F. Brimley, and W. Downes (mainly Hemiptera); A. Cosens (gall-forming insects); R. C. Treherne (Thysanoptera); and C. MacNamara (Collembola). Some of these were amateurs in the true sense in that collecting and studying insects were diversions from their ordinary professional life, while others were professional entomologists who carried on studies in systematics on a hobby basis as opportunity offered.

However, professional systematic entomology in Canada really began between 1915 and 1919 with the establishment of the Canadian National Collection of Insects and the development of a staff of systematists in the federal service. The National Collection of Insects, which now comprises a main collection in the Science Service Building at Ottawa and a number of regional collections at laboratories of the Forest Biology and Entomology divisions, began as two basic collections. The first, that of the Entomological Branch, dated back to 1887, when James Fletcher was appointed as the first Dominion Entomologist and Botanist and donated his own personal collection as a nucleus on which to build. It was soon supplemented by the collections of Gibson, Harrington, and others, and subsequently by contributions from laboratories of the Branch. The second collection was that of the Biological Division of the Geological Survey, then housed at the National Museum of Canada. It included the material collected on the Canadian Arctic Expedition of 1913-18 and several important private collections. In 1915 arrangements were made to coordinate the work of the Branch and of the National Museum, their joint collections to be considered henceforth as the Canadian National Collection of Insects. It had been the intention to incorporate the Branch collection into that of the National Museum, but because of congestion at the Museum, which was then occupied by Parliament (the Houses of Parliament having been destroyed by fire in 1916), it was eventually decided to reverse the procedure, and in 1917 the unification of the federal insect collections was completed, and the responsibility for their future development fell to the Department of Agriculture.

In 1919, J. H. McDunnough, lepidopterist, was appointed Chief of the Division of Systematic Entomology, with responsibilities of developing the Collection and the Library, of providing an identification service, and of conducting original researches in systematic entomology. During the next few years a small supporting staff was developed, but by 1931, when the headquarters of the Entomological Branch moved from the Birks Building to the Confederation Building, the systematic staff consisted of only three specialists (McDunnough, W. J. Brown, and G. S. Walley), although there were a number of enthusiastic systematists elsewhere in the Branch, notably J. M. Swaine, Ralph Hopping, and Norman Criddle, who were coleopterists, and C. R. Twinn and Eric Hearle, who studied the systematics of biting flies. By contrast, the staff of the Insect Systematics and Biological Control Unit now includes 23 specialists (Lepidoptera, 4; Hymenoptera, 6; Diptera, 5; Coleoptera, 4; Hemiptera, 3; and Siphonaptera, 1; with some of the officers conducting part-time investigations in other orders). In addition, several officers at field laboratories of the divisions of Entomology and Forest Biology maintain a part-time interest in the systematics of a number of groups, including several such as ticks, spiders, and mites that at present are not under investigation by the Ottawa group.

Although Canadian universities have not been noted as sources of major contributions to insect systematics, there are some important exceptions, among which the researches of E. M. Walker of Toronto on Odonata and Orthoptera stand highest. Many years ago, Dr. Walker[25] enjoyed the privilege that comes to few these days of discovering an insect of ordinal or near-ordinal distinction. This insect, the immensely interesting orthopteroid *Grylloblatta campodeiformis*, has been chosen as the "Congress insect" of the Tenth International Congress of Entomology. Other university teachers who have made contributions to systematics are W. A. Clemens, F. Ide, and C. E. Atwood of Toronto, J. G. Rempel of

25 *Canadian Ent.* 46: 93-99, 1914.

Saskatchewan, E. H. Strickland of Alberta, G. J. Spencer of British Columbia, Gustave Chagnon and Brother A. Robert of Montreal, and H. H. J. Nesbitt of Carleton College, Ottawa.

Even identifying indigenous Canadian insects frequently requires that systematists have knowledge of the insect fauna of other parts of the world, especially of the remainder of the Nearctic and of much of the Palearctic region. Many of the species occurring in Canada were described from elsewhere, especially from the United States. Many species, including a large number of economic forms, were introduced from Europe, and many species, especially in northern Canada, are of normal Holarctic distribution. Frequently a species is known by one name in the New World and by another in the Old. The most important tools of the systematist, therefore, are his literature and reference collections of insects. The Canadian National Collection of Insects and the Entomology Division Library, which is associated with it, are the largest and most representative in the country. McDunnough made tremendous contributions to the early development of the Collection and the Library, and both have continued to grow since his retirement. The Collection is developed largely by exchange, purchase, gift, and bequest of specimens, by retentions of material associated with the identification service, and by insect surveys conducted by officers of the Unit and others. The Forest Insect Survey, which started in 1936, has been an invaluable source of material. The Northern Insect Survey, a co-operative project with the Defence Research Board, Department of National Defence, has permitted the investigation of about 60 localities in the Arctic and Subarctic since its inception by T. N. Freeman[26] in 1947. As a result of this survey, the Canadian National Collection has acquired the largest and most representative collection of insects ever assembled from the northern parts of the New World. It will be many years before this mass of material is worked over although investigations are being conducted at present in a number of groups, particularly the biting flies and some other families of Diptera, the butterflies and a few families of Heterocera, some Coleoptera, Hymenoptera, and the fleas.

The Canadian National Collection of Insects at Ottawa now occupies nearly 8,000 drawers in steel cabinets, plus numerous microscope slide cabinets and alcohol containers. It probably contains 3 million specimens and certainly includes representatives of more than 40,000 species. It contains type material of over 7,000 described forms, including about 3,000 holotypes or lectotypes. It contains some important historic material, including the Francis Walker types of Lepidoptera based on the D'Urban collections, and some of Provancher's types of Hymenoptera. There are some other large collections of insects in Canada, the Lyman collection at McGill University and the Provancher collection at the Provincial Museum, Quebec, being of special importance. Several of the universities, especially Alberta, Saskatchewan, and British Columbia, and the provincial museums at Halifax, Victoria, and Toronto maintain significant collections.

The great bulk of published work on the systematics of Canadian insects has been at the species level. Numerous new species in all groups were described as they were discovered, and many distributional lists, some of them on a provincial or national basis, were published. In the early years of the Division of Systematic Entomology an immense productivity of this type was evident. In eight years C. H. Curran published nearly 150 papers on Diptera. Between 1919 and 1946 McDunnough published 153 papers on Lepidoptera, 38 on Ephemeroptera, five on Odonata, two on Diptera, and one on Hemiptera. He reported (1926) that in six years or less he had described 200 new species while Curran had described

26 *Arctic* 7: 275-283, 1955.

250 and H. L. Viereck 286. This was an era of basic descriptive work associated with the elucidation of numerous described species—a tying down of names. It was an era of synoptic accounts of the fauna of local regions, with relatively few revisions of genera or larger groups. These practices reflected contemporary circumstances, one of which was that available collections were woefully unrepresentative. Little of Canada had been surveyed for its insects, so that broad revisions would have been premature.

As time passed, circumstances changed, and the transition continues. The immense insect fauna, perhaps 80,000 species or more, of this huge country is gradually being sampled, and systematists are therefore permitted to work more effectively on a "group" basis. While "piece-work" continues, and is a necessary phase, many research assignments are now aimed towards eventual publication of revisionary studies on as broad a basis as possible. Nevertheless it will be many years before revisions will be appropriate or of lasting value in many if not in most groups. The trend towards more comprehensive studies is represented by Brown's revisions of certain sections of Scarabaeidae (1928 *et seq.*), Elateridae (1933 *et seq.*), and Chrysomelidae (1942 *et seq.*), Walley's revisions of the ichneumonid genera *Smicroplectrus* (1937), *Campoplegidea* (1940), *Syndipnus* (1940), and *Casinaria* (1947), and McDunnough's revisions of the geometrid tribe Cleorini (1920), the Nearctic agrotids (1928), and the genus *Peronea* (1934). Other revisions of moderate scope by officers of Systematic Entomology were those of G. E. Shewell on Lauxaniidae (1938), J. R. Vockeroth on *Aedes* (1954), J. F. McAlpine on Lonchaeidae (in press), A. R. Brooks on root maggots (1951), T. N. Freeman on *Argyrotaenia* (1945), E. G. Munroe on *Calisto* (1950), L. A. Kelton on *Lygus* and allies (1955), B. P. Beirne on *Macrosteles* (1952) and on other genera of leafhoppers, and S. L. Wood on *Carphoborus* (1954). Important contributions from other sources include C. R. Twinn's work on Eastern Canadian black flies (1936), the papers on water beetles by H. B. Leech and J. B. Wallis, and many others of varying scope and significance.

A number of larger works have been undertaken. Earlier samples were McDunnough's check lists of Lepidoptera of Canada and the United States (1938, 1939) and Curran's important manual on North American Diptera (1934), the foundations of which were laid on his work in Canada. More recently, Peck (1951) contributed the chalcidoid portion of a catalogue of Nearctic Hymenoptera, and a number of handbooks on a national or regional basis are being completed. In general the latter deal with the strongly economic groups (leafhoppers, grasshoppers, etc.) and are designed principally for use by field entomologists. Frequently, now, groups are being investigated on a Nearctic basis, and in a few cases world revisions are being undertaken. The change in emphasis from diffuse descriptive work towards revisionary studies and other works of a more philosophical or fundamental nature is only now becoming apparent, and relatively few of the large monographs are actually in print.

Only two orders have been monographed on a Canadian basis: the Odonata, of which only the volume on Zygoptera (E. M. Walker, 1953) has been printed, and the Siphonaptera (G. P. Holland, 1949). The Canadian Ixodoidea have been monographed (J. D. Gregson, 1956) and a revision of Canadian Cicadellidae (B. P. Beirne) is in press. R. Glen (1950) described the wireworms of the genus *Ctenicera* on a world basis; and handbooks by A. R. Brooks on the grasshoppers and adult Elateridae of the Canadian prairies are well advanced. Since his retirement in 1946, J. H. McDunnough has completed and published major papers on the lepidopterous genera *Eupithecia* (1949), *Euxoa* (1950), and *Hydriomena* (1954). F. A. Urquhart, who in 1949 published a book, *Introducing the*

Insect, is completing another book on the Orthoptera of Eastern Canada. Other broad revisionary studies, recently completed or well advanced, include the Nearctic Ctenisicini (W. R. M. Mason, 1955 *et seq.*), the Nearctic Triaspidini (J. C. Martin, 1956), the world Sparganothidinae (R. Lambert), larvae of Nearctic Olethreutidae (M. R. MacKay), the Nearctic *Agriotes* (E. C. Becker, 1956), New World *Chrysomela* (W. J. Brown), Nearctic *Schinia* (D. F. Hardwick), Nearctic *Colletes* (W. P. Stephen, 1954), and the world Scatomyzidae (J. R. Vockeroth). A major long-term project that will not mature for some years, although some contributory papers have already appeared, is a revision of the world genera of Pyraustinae by E. G. Munroe.

In this era of the "new systematics", with the increased emphasis on a biological definition of the species and its components, the standard methods of museum systematics in Canada, as elsewhere, have been supplemented by other disciplines and techniques, especially in the investigation of special problems. Serology and chromatography as well as genetics and cytology are examples of specialties and techniques now used by a number of Canadian investigators. Behaviour patterns, host preferences, and other facets of ethology are compared in interpreting certain problems. Refinements and elaboration of the standard morphological method, including analysis of immature stages as well as more critical examination of minute character differences in adults, are now widely established. Variables are frequently subjected to statistical methods of analysis. Canadian contributions in these fields are only starting, but the work of S. G. Smith, J. W. Boyes, and K. Rothfels in genetics and cytology should be mentioned, along with A. West, A. E. R. Downe, and J. G. Robertson in serology and chromatography. Taxonomic studies on immature stages include those on sawflies (D. E. Maxwell, 1955), wireworms (R. Glen, 1950), Cerambycidae (F. C. Craighead, 1923), bark beetles (J. B. Thomas), grasshopper nymphs (R. H. Handford, 1946), larvae of parasitic Diptera (W. R. Thompson, 1920 *et seq.*), and larvae of Lepidoptera (M. R. MacKay and W. C. McGuffin). W. J. Brown's studies of sibling species of chrysomelids were based on food plant restrictions, distribution patterns, and morphological comparisons of population samples. D. F. Hardwick's nearly completed studies on some Heliothidinae provide an example of a taxonomic study in which extremely detailed comparisons of adults are supplemented by similar analyses of eggs, all stages of larvae, life-histories, host preferences, and distributions. Atwood and Peck's analysis of *Neodiprion* sawflies (1943) was an earlier example in which species were defined by differences in life-history as well as by larval and adult characters.

Truly, systematic entomology in Canada stands at a new frontier today. Much of the pioneering work has been done (though much remains) and we are entering a period characterized by clearer concepts; new tools and techniques; better collections, libraries, and other facilities; and the recognition of the fundamental importance of systematics to all branches of entomological research.

Morphology and Embryology

Canadian entomologists have made many contributions to morphology but relatively few of these are concerned with fundamental problems or theories because the early workers were interested chiefly in systematics and economic entomology. There were few, if any, primarily interested in morphology. Both systematists and economic entomologists, however, have contributed many descriptive and some interpretive studies of structures of insects on which they have worked.

Contributions from the purely morphological point of view came later. Some universities encourage students in entomology to undertake morphological research either as a thesis for a higher degree or as a subsidiary project. The results of many such researches have been published, some of a very high order. This, in part, accounts for the fact that morphological papers are frequently found among the early works of individuals who have since distinguished themselves in other fields of entomology.

Among entomologists with a primary interest in morphology E. M. Walker, University of Toronto, is outstanding for his fundamental contributions to our knowledge of the external genitalia of orthopteroid insects[27] and for several papers on the anatomy of *Grylloblatta campodeiformis*, the primitive orthopteroid which he himself discovered.[28] His interest in morphology has inspired some of his students who also have contributed to this field. Of these, Norma Ford's fine comparative study of the abdominal musculature of orthopteroid insects deserves special mention.

In more recent years J. G. Rempel, University of Saskatchewan, has contributed to our knowledge of the embryology of *Mamestra configurata* Wlk.[29] and he has lately turned his attention to the morphology of the Arachnida. Doreen Maxwell, of the Forest Biology Division, Canada Department of Agriculture, published an admirable monograph on the internal larval anatomy of sawflies. Her paper deals specifically with the structure of the alimentary canal, the Malpighian tubules, and the labial glands. It is a valuable contribution to knowledge of the phylogeny of these insects.

Mention should be made of the excellent contributions in cytology by S. G. Smith, particularly in Lepidoptera and Coleoptera, and by Maxwell on the Diprionidae.

The Canadian entomologist who has most consistently maintained an interest in morphology is Professor E. Melville DuPorte. He has published papers on both internal and external anatomy, his most recent studies being on the morphology of the head.[30] As a result of these studies, he has advanced new theories of the nature and origin of some of the cranial sutures and sclerites. Several of his students have also made contributions to morphology, the most recent being R. S. Bigelow, who, in addition to other papers, has published a valuable study of the facial structure in Hymenoptera.

Cytology and Genetics

The application of cytology and genetics to entomology in Canada began about a quarter of a century ago, although previously limited use of insects had been made in purely cytological and genetic problems such as chromosome behaviour and crossing over. Since 1935, these two disciplines have been of particular value in insect systematics and the study of phylogenetic relationships, and have also contributed to a better understanding of the evolution of genetic systems, chromosome mechanics, and sex-determining mechanisms.

The first major contribution in cytogenetics was the demonstration by S. G. Smith[31] that two species of spruce sawflies co-exist in Europe, as proved by differences in type of parthenogenesis and number of chromosomes, and that only one, *Diprion hercyniae* (Htg.), became established in Canada. Similar cytological criteria supported the taxonomic separation of the bronze poplar borer, *Agrilus liragus* (B. & B.), from the bronze birch borer, *A. anxius* Gory, and of the normal-winged curculionid *Hylobius pinicola* (Couper) from a

27 Ann. Ent. Soc. America 12: 267-325, 1919; 15: 1-87, 1922.
28 Ann. Ent. Soc. America 24: 519-536, 1931.
29 *Canadian Ent.* 83: 1-19, 1951.
30 *J. Morph.* 79: 371-417, 1946.
31 *Sci. Agr.* 21: 245-305, 1941.

vestigial-winged ally, in each case identifying one as the primitive and the other as the derived species. Chromosomal morphology has been used similarly in suggesting the arrangement of species of *Tribolium* into a natural evolutionary sequence. A cytological paradox, the occurrence in certain individuals of a species of chromosomes in excess of the basic diploid set, has been receiving attention by Smith and his associates over the past five years. Since these supernumerary chromosomes have certain qualities in common with sex chromosomes, they are generally regarded as having arisen by replication of genetically inert parts of the sex chromosomes. Evidence is being accumulated, however, that involves the other chromosomes in their origin through retention of the by-products of chromosome fusion. Even if this interpretation is not substantiated by future work, the process of chromosome fusion at least constitutes a mechanism whereby numerical differences arise within and between species.

Comparisons of the bands in the salivary-gland chromosomes of Canadian black flies by K. H. Rothfels and R. W. Dunbar,[32] University of Toronto, and analyses of somatic chromosome complements in some of the higher Diptera by J. W. Boyes and A. W. Wilkes,[33] McGill University and Entomology Laboratory, Belleville, Ont., have been of value in distinguishing taxonomic entities and elucidating phylogenetic relationships. The more recent cytological studies of sawflies attacking forest trees by Smith and by Doreen E. Maxwell, at McGill University, show promise of contributing to the solution of the baffling problem of speciation in the genus *Neodiprion.*

Studies of heredity and variation to date have made much less of a contribution to entomological research, primarily, no doubt, because they are usually long-term studies necessitating rearing through several generations. However, some progress has been made. An analysis by Smith[34] of differences in genetic factors between the jack-pine budworm, *Choristoneura pinus* Free., and the cytologically similar spruce budworm, *C. fumiferana* (Clem.), has shown that natural hybridization does not increase their potential hazards as destructive pests and has suggested the pattern for analysis of the *Neodiprion* complex, through the assessment of various geographical and reproductive isolation barriers. Through the discovery of mutant types of *C. fumiferana,* evidence has been obtained that fecundity and almost certainly voltinism are controlled by multiple factors, or so-called polygenes. This provides a means of studying the dynamics of natural populations that eventually should contribute to a better understanding of recurrent budworm outbreaks.

The development of varieties of wheat resistant to the wheat stem sawfly, *Cephus cinctus* Nort., and the biological significance of parthenogenetic reproduction of the sawfly are being studied at the Canada Experimental Farm and the Science Service Laboratory, Lethbridge, Alta., in attempts to produce a marketable, resistant variety. Solid-stemmed varieties resistant to the sawfly were crossed with non-resistant varieties of superior marketing quality at the Experimental Station, Swift Current, Sask., by H. J. Kemp and by A. W. Platt and Ruby I. Larson with considerable success. An important aspect of the problem, as found by C. W. Farstad and N. D. Holmes, is the variation in the sex ratio of sawflies reared from females of different ages and on different varieties of wheat. Margaret R. Mackay[35] showed that parthenogenetic behaviour in unisexual and bisexual populations appears to be altered by adaptive modifications during meiosis.

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32 *Canadian J. Zool.* 31: 226-241, 1955.
33 *Canadian J. Zool.* 31: 125-165, 1953.
34 *Canadian Ent.* 85: 141-151, 1953.
35 *Canadian J. Zool* 33: 161-174, 1955.

Investigations at the Entomology Laboratory, Belleville, Ont., and the Forest Insect Laboratory, Sault Ste. Marie, suggest that the larch sawfly, *Pristiphora erichsonii* (Htg.), is comprised of an assemblage of bio-types between which gene exchange is prevented by the absence of mating.

Although Canadian workers have obtained evidence that differences in susceptibility of the house fly to DDT are inherited, very little has been done on the genetics of insecticidal resistance.

Physiology and Behaviour

Prior to 1945, very limited study of insect physiology and behaviour was undertaken in Canada. Today, some 40 investigators, representing a dozen universities and museums and as many federal government laboratories, are engaged primarily in this field. Emphasis has centred on the biochemical aspects, particularly of feeding, nutrition, and metabolism. Nevertheless, the range of interest is surprisingly broad and is not fully represented by the topics covered in the summary accounts that follow.

Nutrition and Metabolism

Research in Canada on insect nutrition and metabolism has increased greatly during the last decade. Studies on the nutritional requirements of representative species of insects and the effects of food components on physiological activities have been conducted at five or six universities and in a number of government laboratories. Work on metabolism has been undertaken at almost as many centres. More than half of the work on metabolism and about three-quarters of that on nutrition has been done in government laboratories in association with projects of an applied nature.

Highly refined artificial diets and aseptic culture techniques have been devised and used widely to determine the requirements of a number of insects for growth, development, and reproduction. H. L. House,[36] working with *Pseudosarcophaga affinis* (Fall.), has determined for the first time the requirements of an entomophagous insect. This work has opened the field for studies of nutrition and metabolism with insect parasites and has also provided a basis for rearing parasites for biological control and other purposes. Similar pioneer work has been done by W. G. Friend,[37] Entomology Laboratory, Ottawa, with a phytophagous species, *Hylemya antiqua* (Mg.). A. Lemonde and R. Bernard, Laval University, have investigated the biochemistry of metamorphosis of *Tribolium confusum* Duv. These investigations have not yet established nutritional differences that have systematic significance. A. J. Thorsteinson,[38] University of Manitoba, has shown that certain mustard oil glycosides stimulate the feeding response in the diamondback moth, *Plutella maculipennis* (Curt.). No nutritional activity has been demonstrated for these compounds. For most species, about 30 dietary ingredients are necessary, namely: 12 amino acids, 10 *B*-complex vitamins, cholesterol, glucose, ribonucleic acid, and a number of salts; however, requirements for special micronutrients have yet to be determined. This information is fundamental to work on other problems, such as varietal resistance of plants to insects. For example, J. L. Auclair and J. B. Maltais, Science Service Laboratory, St. Jean, Que., have shown that a variety of pea susceptible to attack by the pea aphid, *Macrosiphum pisi* (Harris), contains a higher concentration of the essential amino acids than do more resistant varieties. An attempt is being made to determine the exact nutritional requirements of the aphid. In addition, work on salivary and digestive enzymes and food absorption and transformation, which

36 *Canadian J. Zool.* 32: 331-341, 1954.
37 *Canadian J. Zool.* 34: 152-162, 1956.
38 *Canadian J. Zool.* 31: 52-72, 1953.

may be of value in the fields of nutrition and metabolism, is being done at several centres on various insects.

The need for fundamental investigations on insect metabolism became necessary mainly as a basis for determining the modes of action of toxicants. Investigations on various mechanisms for the anaerobic degradation of carbohydrates in different insects are in progress, mainly at the Science Service Laboratory, London, Ont. Some notable results have been achieved by W. Chefurka[39] on the mechanism of the "glucose-monophosphate shunt". B. N. Smallman and his associates have shown that acetylcholine, which is involved in the synaptic transmission of nerve impulses in vertebrates, occurs in insects[40] and they have defined the enzymatic mechanism for its resynthesis.[41] These investigations, and others by A. J. McGinnis, Science Service Laboratory, Lethbridge, Alta., S. E. Dixon, Ontario Agricultural College, and P. Faulkner, Forest Insect Laboratory, Sault Ste. Marie, Ont., have resulted in the identification of a number of enzymes and have located the sites of activity of many in different tissues; as a result, the natures of these complicated biochemical systems are more clearly understood. Other investigations include work on respiratory metabolism, the organic role of the fat body, and purine excretion.

Insect Blood

Canadian research on insect blood is confined largely to the past decade and to laboratories in the Entomology and Forest Biology divisions of the Canada Department of Agriculture. Emphasis has been upon the functions of the cellular elements and the bio-chemical aspects.

A beginning has been made by J. W. Arnold on a basic classification of blood cells. His most intensive work[42] has been on the haemocytes of the Mediterranean flour moth, *Anagasta kühniella* Zell., which he grouped into four classes. He also showed that, largely as a result of mitotic activity of one cell class, the spheroidocytes, the total number of cells increased with the onset of pupation, with recovery from sublethal dosages of certain fumigants, and with certain other conditions of stress. J. A. Muldrew demonstrated the importance of phagocytes in a resistant strain of the larch sawfly, *Pristiphora erichsonii* (Htg.), in encapsulating and inhibiting development of eggs of the parasite *Mesoleius tenthredinis* Morley.

W. F. Baldwin and H. L. House examined the variation in the specific gravity and osmotic pressure of the blood of several species of insects in relation to parasitism and to acclimation at high temperatures. Further definitive studies are required before generalizations can be made.

Some of the most noteworthy investigations on insect blood, principally of its bio-chemistry, are being carried out at the Insect Pathology Laboratory, Sault Ste. Marie, Ont. Of particular significance are the work of P. Faulkner[43] with enzymes in the blood of the silkworm, *Bombyx mori* (L.), that of A. M. Heimpel[44] concerning the pH of the blood and gut of a number of forest insects, and that of G. R. Wyatt, T. C. Loughheed, and S. S. Wyatt[45] in determining the individual organic components of silkworm haemolymph. S. S. Wyatt recently developed a physiological solution for the *in vitro* culture of silkworm ovarian tissue. These investigations are directed towards an understanding of the pathogenicity of bacteria and viruses in insects.

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39 *Enzymologia* 17: 73-89, 1954.
40 *Nature* 175: 946, 1955.
41 *J. Physiol.* 132: 343-357, 1956.
42 *Canadian J. Zool.* 30: 352-364, 365-374, 1952.
43 *Biochem. J.* 60: 590-596, 1955.
44 *Canadian J. Zool.* 33: 99-106, 1955; 34: 210-212, 1956.
45 *J. Gen. Physiol.* in press.

Although research in this field has arisen independently in several laboratories with specific and somewhat unrelated problems, increased interest in the physiological activities of the blood as a tissue is stimulating greater integration in investigation.

Serology

Serological methods have aided in the solution of entomological problems in Canada. The earliest Canadian work was done by J. G. Rempel, University of Saskatchewan, and his associates of the Saskatchewan Department of Public Health. In 1946, they[46] applied precipitin-test techniques to studies of the feeding habits of *Aedes* mosquitoes and their relation to the transmission of western equine encephalomyelitis virus in Western Canada. Since then the precipitin test has been used rather extensively in determinations of the blood meals of haematophagous Diptera.

More recently, the application of serological techniques to entomological problems has been widely investigated at Queen's University, where A. S. West and his associates have developed methods for determining the hosts of entomophagous insects. At present they are investigating the serological activities of insect antigens, especially with respect to the reactions of hosts to mosquito and black fly bites.

A. E. R. Downe is using the precipitin test to determine the rate of digestion of blood in mosquitoes and other biting flies and to clarify the host preferences of such pests. Serological techniques for the specific identification of bird bloods[47] are being developed in connection with these studies.

The serological relationships of insect blood, insect viruses, and virus inclusion material are being studied at the Insect Pathology Laboratory, Sault Ste. Marie, Ont.

Diapause

The climatic diversity in Canada has on occasion allowed introduced as well as native insects to take advantage of wide potentialities for diapause. The European spruce sawfly, *Diprion hercyniae* (Htg.),[48] and the European corn borer, *Pyrausta nubilalis* (Hbn.),[49] have potentialities for both single and multiple generations each year. A univoltine strain of the sawfly, which undergoes a long, obligatory diapause, is able to maintain itself in colder regions where a second generation could not survive; the multivoltine strain predominates in warmer areas. The univoltine strain provides the small and stable but dependable and safe element of the population, whereas the multivoltine strain is likely to produce violent oscillations in abundance. In both species, individuals with potentialities for more than one generation a year may produce a second generation when the season is favourable.

Investigations at Lethbridge into the nature of diapause in the wheat stem sawfly, *Cephus cinctus* Nort., were sparked by the discovery in 1938 that extreme drouth conditions during the previous spring caused a reinstatement of diapause, resulting in a two-year life-cycle. In the fall, full-grown larvae enter an obligatory diapause that is dissipated by chilling during fall and early winter, optimally at a temperature near 10°C. Higher temperatures are needed for post-diapause development. However, temperatures above 30°C. reimpose diapause if they are applied at a critical time during the early phases of post-diapause devlopment.[50] N. S. Church[51] showed that heat inhibits secretion of the growth

46 *Canadian J. Res.*, E, 24: 71-78, 1946.
47 *Nature* 176: 740-741, 1956.
48 *Canadian J. Res.*, D, 19: 295, 346, 350, 362, 417, 454, 1941.
49 83rd Ann. Rept. Ent. Soc. Ont. (1952): 43-47, 1953.
50 *Canadian J. Res.*, D, 25: 66-86, 1947.
51 *Canadian J. Zool.* 33: 339-369, 1955.

and differentiation hormone by the prothoracic glands and destroys any of this hormone that has been produced at more favourable temperatures. Unless the titre of the hormone is adequate the prothoracic glands revert to dormancy, and this is broken only when subsequent chilling induces the neurosecretory cells of the brain to secrete and re-initiate the post-diapause chain of events. In nature this involves hibernating through a second winter. The role of dryness in the reinstatement of diapause was initially a complicating factor. It was later established that desiccated larvae must absorb moisture before being able to begin post-diapause development, but that dryness itself had no effect on diapause development. If desiccation were severe it prevented post-diapause development even after moist conditions were restored, and such larvae did not respond to chilling as did larvae in diapause Hence the developmental block induced by excessive dryness is not a true diapause but is rather an injury.

Cold-hardiness

Although the field of insect cold-hardiness has been neglected since the late 1920's, when it was explained in terms of bound water, it has appropriately received serious attention in recent years in Canada. This work is centred at Lethbridge. Rejection of most of the older work, chiefly on the ground of technical error but sometimes because of misinterpretation, formed an important preliminary step. Measurement of cold-hardiness in terms of supercooling is one of the few surviving concepts. With this as a starting point, the action of contact moisture in reducing supercooling by "inoculating" the freezing process was a major advance. Originally, contact moisture was considered as any moisture adhering to the insect, whether from the hibernaculum or from the excretions of the insect itself. Later it was realized that food acted as contact moisture and the lack of cold-hardiness of feeding insects was thereby explained. Still later the role of air-borne particles that initiated freezing in the contact moisture of food and thereby also in the insect brought a common explanation to all cases of reduced supercooling. Thereafter, the authentic cases of increased supercooling, or cold-hardening, became very few. In addition, some of these were without significance since they passively accompanied developmental changes in warm weather, e.g., during moults. The genuine occurrence of cold-hardening is confined to situations where internal changes produce increased supercooling during hibernation.[52] These may be directly internal, as those produced by developmental processes, or indirectly internal when caused by the action of environment. In the latter category, temperature is often responsible for cold-hardening through its influence on developmental processes; subdevelopmental temperatures have not been proved to be effective. The only other environmental factor likely to produce cold-hardiness, namely dryness, acts in a purely physical manner; to the extent that water loss concentrates the body fluids and depresses the freezing point, it also depresses the supercooling point. The amount, however, is negligible.

The various tissues of an insect freeze within a very narrow range, usually within a degree or two below 0°C. By a new technique, the amount of ice in an insect at any given temperature may be determined. This has provided further evidence against the occurrence of appreciable amounts of bound water, and in any case the assumed protective action of bound water is very questionable.

Nucleation phenomena, in explaining the initiation of freezing, have placed on a rational basis the effects of time on supercooling. Freezing of supercooled insects at temperatures above their supercooling points is dependent on the

52 *Canadian J. Zool.*, in press.

formation of ice crystal nuclei through chance molecular orientations of favourable nature; consequently probability and time are major factors.

On the practical side, investigations elsewhere have shown that low temperature is a limiting factor in the survival of many species throughout Canada. For example, in the Maritime Provinces the oystershell scale, *Lepidosaphes ulmi* (L.), is not usually influenced to any great extent by cold, but at least one of its major parasites is held down by winter mortality in the colder part of its range, though not in the warmer areas. In the Rocky Mountains, winter mortality of the lodgepole needle miner, *Recurvaria* sp., has been directly related to low temperatures. The intricate pathways of cold air currents, both horizontal and vertical, found in mountainous areas are reflected in the pattern of winter mortality.

Insects as Vectors of Plant Viruses

The only Canadian discovery of an arthropod vector of a plant virus was made by J. T. Slykhuis,[53] a plant pathologist who found that the wheat curl mite, *Aceria tulipae* (Keif.), transmitted the wheat streak mosaic virus in Alberta. All other arthropod-borne plant viruses and their vectors known to occur in Canada were first reported from other countries.

Plant pathologists have found that insect-borne diseases cause losses to most crops. Entomologists began to stress the importance of insects as vectors about 20 years ago; but only during the past ten years has serious attention been given and then only by a few workers in the Entomology Division of Science Service. Thus far, emphasis has been chiefly upon aphid vectors, for in Canada as in other countries aphids are the largest and most important group of potential carriers.

The first Canadian work that directly concerned insect vectors of plant viruses began soon after the introduction of the "wonder" insecticides such as the chlorinated hydrocarbons and the organophosphates. Some of these reduced numbers of aphids so greatly that it seemed they must also limit the spread of aphid-borne viruses. But experiments have failed to prove this assumption. For example, there was little reduction in spread of leaf roll virus and virus Y in potatoes treated regularly with DDT, though only occasional aphids were found on treated plants compared with thousands of aphids per plant on untreated controls. This early approach has been followed by long-term field investigations of ecological factors affecting the spread of such diseases.

In laboratory studies, R. H. Bradley[54] is clarifying how aphids transmit potato virus Y, this type of transmission being regarded as typical of the majority of aphid-borne viruses. It has been shown that the green peach aphid, *Myzus persicae* (Sulz.), acquires and transmits virus Y when the mouth parts are inserted in turn into the epidermis of infected and healthy plants. The entire process of transmission takes about one minute. Moreover, though the aphids normally imbibe their food from the vascular tissues, they rarely become infective with virus Y or transmit it after the mouth parts penetrate beyond the first layer of plant cells. Virus Y that is transmitted is carried near the tip of the aphid's stylets. This was shown after it was discovered that the stylets of living aphids could be bared beyond the end of the labium by simple manipulations with capillary tubes. With these methods, it is possible for the first time to study aphid-borne viruses as they are being transmitted by their vectors.

Other investigators have recently begun to study the aphid transmission of potato leaf roll virus, which is very different from that of potato virus Y. In co-operation with plant pathologists, entomologists are making extensive tests to find the vectors of certain viruses for which there is evidence of natural spread

53 *Phytopathology* 45: 116-128, 1955.
54 *Canadian J. Microbiol.* 1: 787-793, 1955.

by insects or other arthropods. In Ontario, these tests are for the vector of cherry yellows virus and in British Columbia for the vectors of two stone fruit viruses and that of witches'-broom of potatoes. At the federal plant pathology laboratory at Vancouver, B.C., considerable progress has been made in the last ten years in determining the virus diseases present in strawberries and raspberries and in laboratory techniques for transmission of them by their aphid vectors.

Behaviour

Until about ten years ago, Canadian work on insect behaviour was restricted mainly to relatively isolated series of observations that formed parts of more extensive studies of bionomics. In recent years, however, there has been a steady increase in the amount of intensive research on behaviour problems. Much of the recent work has utilized pest species, and two major benefits have been derived from this approach. First, the increase in taxonomic diversity has provided sounder information on fundamental aspects of sensory physiology than was provided hitherto by the reactions of only a few species tested repeatedly by different investigators. Secondly, thorough investigation of all facets of the life of an important pest is proving to be a more direct route to sound control measures than were superficial investigations spurred by temporary economic pressures.

One recent improvement common to behaviour studies in which the physical environment is even remotely involved stems from our growing recognition of the fact that most insects operate in well-defined microenvironments where climates differ markedly from those at the human level. More investigators, therefore, are using climatic records taken in the niches where the insects live. This approach has been associated with greater efforts to investigate problems of sensory physiology in natural surroundings as well as in the laboratory although, until recently, integrated laboratory-field attacks on these problems have occurred most often in investigations of reactions to changes in physical factors such as temperature, moisture, atmospheric pressure, and light.

A knowledge of reactions to these physical variables, particularly those responses that lead to changes in the distribution of insects on their host plants or to the adoption of particular directions of travel during active periods, has proved to be an especially valuable aid to forest entomologists concerned with sampling techniques or with other aspects of population dynamics. With this in mind, W. G. Wellington, G. W. Green, C. R. Sullivan, W. R. Henson, and their associates have been conducting a series of investigations[55] to establish the factors involved in the directed movements of larvae of the spruce budworm, *Choristoneura fumiferana* (Clem.), the spotless fall webworm, *Hyphantria textor* Harr., and various species of sawflies and tent caterpillars. Temperature and evaporation preferences have been determined as an aid in interpretation of field behaviour, and effects of overheating, desiccation, starvation, and age on reactions to light have been examined in relation to conditions in particular environments. More recently, the relative importance of polarized light, wind, and radiant heat in determining the orientation of travelling insects has been explored more fully outdoors.[56]

Behaviour involved in host selection has occupied the attention of several investigators. A. W. A. Brown, University of Western Ontario, and his students have studied the responses of female *Aëdes* mosquitoes to natural and "robot" hosts and to colours,[57] and D. M. Davies,[58] McMaster University, has

[55] *Canadian Ent.* 80: 56-82A, 1948; 85: 297-310, 1953; 207-222, 261-274, 1954.
[56] *Canadian J. Zool.* 29: 339-351, 1951.
[57] *Bull. Ent. Res.* 42: 535-541, 1951: 43: 567-574, 1953; 45: 67-78, 1954.
[58] *Canadian J. Zool.* 29: 65-70, 1951.

observed the responses of *Simulium venustum* Say to coloured cloths. L. G. Monteith,[59] Entomology Laboratory, Belleville, Ont., recently gave a very full account of the role of olfactory and chemotactic responses in changes in the preference of the insect parasite *Drino bohemica* Mesn. for its hosts and their food plants. The chemotactic basis of host plant selection has been considered in more general terms by A. J. Thorsteinson,[60] University of Manitoba, who has outlined several avenues for investigation.

The flight behaviour of insects has received somewhat less attention, primarily because of the field problems involved. W. O. Haufe,[61] now of the Science Service Laboratory, Lethbridge, Alta., investigated the flight responses of *Aëdes* mosquitoes to changing atmospheric pressure in the laboratory. B. Hocking's (University of Alberta) well-known study[62] of the flight of insects was, of necessity, primarily a laboratory investigation to determine intrinsic range, speed, fuel consumption, and metabolic rates. Nevertheless, it was carried out against a background of determinations of seasonal changes in the nectar production of the northern flowers that supply fuel for flight, and this production in turn was related to seasonal changes in biting fly populations to give the whole investigation proper ecological perspective. A somewhat similar investigation of the flight of bark and ambrosia beetles in relation to stage of adult development is currently being carried out by J. A. Chapman, Forest Biology Laboratory, Victoria, B.C. J. A. Downes,[63] Entomology Division, Ottawa, has studied the visual control of flight in *Culicoides* and *Aëdes* and, in particular, has shown that the male swarms of these and other Nematocera are determined by a response to characteristic landmarks. The swarming of the males and the discovery of the swarms by the females is considered to be the first stage in the meeting of the sexes; the final recognition takes place within the swarm and depends on an auditory response of the male to the flight tone of the female. Other investigations of insect flight, such as those by W. R. Henson and by D. O. Greenbank,[64] Sault Ste. Marie, on the spruce budworm have been less concerned with behaviour than with the physical agencies involved in dispersal or with the importance of that dispersal to local populations.

Insect Pathology

Early studies of insect diseases were directed mainly towards control of those causing epidemics among such domesticated species as the silkworm and the honey bee. The earliest Canadian study of a disease controlling an injurious species is that of H. T. Güssow,[65] who, in 1911, published an account of the fungus *Isaria farinosa* (Dicks.) Fr. parasitizing the larch sawfly, *Pristiphora erichsonii* (Htg.). C. G. Hewitt[66] discussed the part played by diseases in the natural control of the same insect. Officers of the Canada Department of Agriculture have continued to do most of the work in this field.

Numerous references to observations of disease among insect populations and their importance as control agents occur in the literature of the next 25 years. In 1915, E. M. DuPorte,[67] Macdonald College, reported tests carried out with bacterial diseases of tent caterpillars and white grubs in what appears to have been the first Canadian attempt to assess the effectiveness of insect diseases in control. In 1917 DuPorte and J. Vanderleck[68] investigated the pathogenicity

59 *Canadian Ent.* 87: 509-530, 1955.
60 *Canadian J. Zool.* 31: 52-72, 1953.
61 *Bull. Ent. Res.* 45: 507-526, 1954.
62 *Trans. Roy. Ent. Soc. London* 104: 223-345, 1953.
63 *Trans. Roy. Ent. Soc. London* 106: 213-236, 1955.
64 *Canadian J. Zool.*, in press.
65 Trans. Roy. Soc. Canada, 3rd Ser., 4 (Sec. 4): 95-99, 1911.
66 Canada Dept. Agr., Expt. Farms Bull. 10, 2nd Ser., 1912.
67 7th Ann. Rept. Que. Soc. Prot. Plants (1914-15): 81-85, 1915.
68 Ann. Ent. Soc. America 10: 47-62, 1917.

of *Coccobacillus acridiorum* d'Herelle and other intestinal parasites of locusts. A. G. Dustan,[69] over a period of three or four years, studied fungi of the genus *Entomophthora* as control agents for the apple sucker, *Psylla mali* (Schmdb.), and the green apple bug, *Lygus communis novascotiensis* Knight, in Nova Scotia, and propagated and distributed these fungi in apple orchards. This was the first major attempt to utilize pathogens, but apparently added little to the natural control exercised by the fungi. F. C. Gilliatt recorded some observations on *E. sphaerosperma* Fres., also a parasite of *P. mali.* A. D. Pickett[70] transferred the fungus *E. grylli* Fres. under conditions of high humidity from a heavily infected grasshopper population to one that was relatively free from infection, and reported a considerable decline in numbers in some areas. The fungus was effective also the following year.

Between 1938 and 1946 several important epizootics occurred naturally among major forest insect pests. The most spectacular of these was the accidentally introduced polyhedrosis that controlled the outbreak of the European spruce sawfly, *Diprion hercyniae* (Htg.), in the Maritime Provinces, Quebec, and the northeastern States. This has been described in detail by R. E. Balch and F. T. Bird.[71] Bird continued intensive studies of this disease, and his work is generally looked upon as marking the real beginning of applied insect pathology in Canada. About the same time outbreaks of three forest insects in British Columbia were checked by polyhedroses: *Hemerocampa pseudotsugata* McD. in 1939, *Acleris variana* (Fern.) in 1944 and 1945, and *Lambdina fiscellaria lugubrosa* (Hlst.) in 1946.

With this evidence that disease could be of importance in the control of insects, disease investigations were begun at the Forest Insect Laboratory, Sault Ste. Marie, Ont., in 1946. To provide adequate space and facilities, the Insect Pathology Laboratory was constructed, largely through the efforts of J. J. deGryse, who was then directing investigations in forest entomology in Canada, and it was occupied in 1950. About the same time a section for the study of diseases of agricultural insects was set up in conjunction with the Dominion Parasite Laboratory, as it was then known, in Belleville, Ont. Because of space limitations the latter unit operated at Queen's University, Kingston, Ont., until 1955, when new quarters were provided in Belleville.

The current research program of the Insect Pathology Laboratory falls into four major phases:—

(a) A general survey of diseases of insects, chiefly those attacking forest trees, in collaboration with the Forest Insect Survey. This has revealed the frequent occurrence of disease among insect populations, but in the great majority of cases, especially when the host insect occurs only in enzootic numbers, the disease organism is not sufficiently virulent to play a striking role in population control, although it is fairly certain that some influence is exerted.

(b) Basic studies on the taxonomy, development, and physiology of entomophytic bacteria, fungi, protozoa, and viruses. The life-cycle of insect viruses is gradually being elucidated, and some problems in the taxonomy of fungi, among others, have been clarified.

(c) Investigations of host-parasite relations, histopathology, host specificity, mode of action, etc. Recent interesting developments have been the discovery that the gut pH of the insect is important in determining whether certain bacteria can attack and kill the insect, and that closely related strains of bacteria differ markedly in their host relationships.

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69 *J. Econ. Ent.* 20: 68-75, 1927; 15th Ann. Rept. Que. Soc. Prot. Plants (1922-23): 61-66, 1923.
70 *Canadian Ent.* 6: 24-27, 1935.
71 *Sci. Agr.* 25: 65-80, 1944.

(d) Utilization of disease organisms in the control of forest insects. Although successful experimental introductions of the *D. hercyniae* virus into Quebec, Ontario, and Newfoundland have been reported by Balch[72] and Bird,[73] the first intensive study of introduction and dissemination was that by Bird[74] of the polyhedrosis of *Neodiprion sertifer* (Geoff.) in southwestern Ontario. This virus was introduced into polyhedrosis-free populations, where it quickly became established and caused severe epizootics that re-appeared in successive years and held the populations at low levels. It has been distributed to investigators in the United States for testing, and they report similar results. Observations of infected populations of *D. hercyniae* during 16 years and of *N. sertifer* during six years give no indication of a reduction in virulence of these two viruses.

The Belleville laboratory follows a similar program against agricultural pests. A general survey is carried out to detect new or virulent pathogenic agents. Much effort has been devoted to the possibility of grasshopper control, and this has included not only field studies of application of pathogens, especially *Pseudomonas aeruginosa* (Schroeter) Migula, but also studies on the bacterium itself: survival, effect on the host, determination of dosage, enhancement of virulence, strain variation, etc. Attempts have been made to use *Bacillus cereus* Fr. and Fr. to control the codling moth,[75] but the results have been disappointing.

Studies in insect pathology are just becoming firmly established in Canada. Knowledge of the field is increasing rapidly, and development of new techniques promises even more significant advances in the future.

Insect Toxicology

Chemical methods of crop and forest protection from insect pests have been greatly extended in Canada during the past decade. The vast acreages of forest and prairie made the logistics of sprays and dusts a problem incapable of solution until the discovery of insecticides of such potency that a few ounces per acre was enough to give rewarding results. In the case of the forest, particularly, the advent of air application was an important supplementary development. Consequently, attention to the problems of insect toxicology came comparatively late in Canada, though there is pioneer work worthy of mention. The contributions recorded were made by officers of the Canada Department of Agriculture, unless otherwise noted.

In the early years of this century the Annapolis Valley of Nova Scotia produced annually over a million barrels of apples, a yield that declined during the First World War, largely through the use of lime-sulphur for scab control. By 1921 Bordeaux mixture had come into general use and apple yields had doubled, though insect damage remained a problem. During the next ten years Nova Scotia was the testing ground for a number of developments that had a deep effect on orchard spray practices until the modern insecticides provided alternative methods. The development of the arsenical dusts owes much to this work by A. Kelsall and his colleagues in Nova Scotia, and although the Bordeaux-arsenic dust composed of quick lime, copper sulphate, and white arsenic is now only of historical interest it was a forerunner of the calcium arsenate and the copper-lime dusts still in use today. In the light of present knowledge of the phytotoxic properties of these components, it is not surprising that spray damage was an obvious defect to be overcome. It was in Nova Scotia that the device of reducing arsenical damage by adding ferrous or aluminum sulphate to the

72 Canada Dept. Agr., Forest Insect Investig. Bi-Monthly Prog. Rept. 12(5): 1, 1946.
73 Canada Dept. Agr., Forest Biol. Div. Bi-Monthly Prog. Rept. 10(1): 2-3, 1954.
74 *Canadian Ent.* 85: 437-446, 1953; 87: 124-127, 1955.
75 *Canadian Ent.* 85: 8, 1953.

lime-sulphur-lead arsenate spray was tested and recommended.[76] It seems a logical development from this detailed attention to the effect of the insecticide upon the crop plant to the more recent emphasis, by A. D. Pickett and his co-workers in Nova Scotia, of the effects of sprays on the biological environment of the apple orchard. More recently, J. Marshall and his associates at Summerland, B.C., have contributed materially to better chemical control in orchards in the Okanagan Valley, especially in improved formulations and methods of application. The development of the concentrate orchard sprayer has been a notable achievement. Similarly, an important advance was made in a different field when B. Berck *et al.*[77] revealed that the effectiveness of DDT in the control of black flies in streams depends upon the adsorption of the chemical on the silt particles that are ingested by the larvae.

In the prairies the control of grasshoppers, cutworms, and wire-worms were among the most serious and most difficult entomological problems. The extent and nature of the damage were such that cultural methods promised the more practical way of control and the early use of chemicals was confined largely to poisoned baits. Little of fundamental importance in toxicology emerged from this work and the extension of chemical methods had to await the discovery of the extremely effective chlorinated hydrocarbons. The success of the newer materials is illustrated by the effective seed dressings and soil applications for the control of wireworms and root maggots achieved at several laboratories, notably at Saskatoon; and by the success in spraying with ground equipment and aircraft against grasshoppers, first demonstrated in co-operative experiments with the Entomology Section of the Defence Research Board Experimental Station at Suffield, Alta.[78] Such successes provided a direct stimulant to fundamental enquiry on why these compounds were so effective, and basic toxicological work was undertaken first in the zoological departments of the universities and later in the federal government laboratories.

At Macdonald College wartime studies on insecticidal activity led to some of the earliest work on the properties of the DDT molecule responsible for its toxicity to insects.[79] Refinements of the bioassay methods developed include the now well-known *Drosophila* test,[80] and a micromethod of application that enabled the study of the effect of site of application on insecticidal efficiency.[81]

Comparative studies by A. W. A. Brown and his students at the University of Western Ontario, with cockroaches as test insects, have shown that the majority of modern insecticides, and all the chlorinated hydro-carbons, initially cause an increase in metabolic rate, and that they increase the spontaneous action potentials of nerve; many have a long latent period before action potentials and metabolism are increased.[82] None of the chlorinated hydrocarbons tested are anticholinesterase in action, and outside the organic phosphates only pyrolan is so active. The great majority of insecticides (22 out of 26 tested, including DDT and methoxychlor) inhibited cytochrome oxidase *in vitro*, but did not materially decrease the level of the enzyme *in vivo*.

At the Ontario Agricultural College E. H. Salkeld showed that DDT-treated crops were not repellent to honey-bee workers but that ingestion of DDT resulted in a histopathology of the mid-gut epithelium,[83] and new aphicides are being investigated by a special screening method.

76 68th Ann. Rept. Nova Scotia Fruit Growers' Assoc., pp. 25-31, 1931.
77 *Canadian J. Agr. Sci.* 33: 379-393, 1953; *Anal. Chem.* 25: 1253-1256, 1953.
78 *J. Econ. Ent.* 40: 276-277, 1947.
79 *Can. J. Res.*, D, 25: 12-44, 1947.
80 *Canadian Ent.* 86: 562-569, 1954.
81 *Canadian J. Zool.* 30: 254-266, 1952.
82 *Canadian J. Zool.* 32: 74-81, 1954.
83 *Canadian Ent.* 83: 53-61, 1951.

The various diphenyl compounds and organic phosphates have been evaluated by T. Armstrong, Vineland Station, Ont., as acaricides for use in Canadian orchards.[84]

Direct participation in toxicological work by the federal department, as distinguished from the general *ad hoc* work, was first secured through the collaboration of the Defence Research Board, Department of National Defence. The facilities of the Suffield Experimental Station were promptly used by H. Hurtig and his associates for studies of insecticide application,[85] not only for forest protection[86] but also for the more distinctively Canadian problem of personnel protection from biting flies.[87] A Science Service laboratory,[88] built on the campus of the University of Western Ontario and occupied in 1951, was assigned basic work on the long-term effects of agricultural chemicals on the ecology of the crop, a broad subject of which the toxicology of insecticides is an essential part. The bioassay work necessary for evaluation of commercial formulations of insecticides submitted for registration under the Pest Control Products Act was allocated in 1952 to the new Pesticide Testing Laboratory, Plant Products Division, built on the Central Experimental Farm, Ottawa. Individual laboratories of the Entomology Division contribute much field data required for registration of new materials.

Among the main achievements of the London laboratory is the verification by B. N. Smallman and W. Chefurka that the insecticidal action of the organophosphorous compounds is similar to the process of mammalian toxicity by the demonstration of the presence in insects of choline acetylase[89] and of acetylcholine.[90] This supported by the previous demonstration of the existence of a group of cholinesterases, removes doubts at one time current that these agencies are vital to nerve transmission in insects. The peculiar selectivity of schradan, a systemic phosphorous insecticide that is effective for the control of sap-feeding but not of leaf-eating insects, has been shown by E. Y. Spencer and R. D. O'Brien to be due to an *in vivo* conversion of schradan to an anti-cholinesterase[91] that present evidence indicates is produced in susceptible insects within the nerve cord, whereas in resistant insects it is produced outside the nerve tissues and is hydrolyzed into inert products before it can phosphorylate the cholinesterase. A detailed study of glycolysis in Diptera has not shown any departure from the Embden-Meyerhoff process in vertebrates sufficiently marked to provide a basis for the derivation of insecticides non-poisonous to mammals.[92] Moreover, the direct oxidative pathway through sedoheptulose-7-phosphate has been found in the oxidation of glucose in the flight muscle of house flies.[93] A by-product of studies on bacterial dissociation is the discovery by C. L. Hannay that the pathogenicity to insects of certain forms of *Bacillus cereus* F. and F. is coupled with the production by the bacteria on sporulation of an inclusion body, protein in character and toxic to those species of insect with guts of sufficient alkalinity to disperse the protein.[94]

Population Dynamics

Until recently Canadian contributions to population dynamics have been few. For example, in the review by Solomon,[95] which is one of the few dis-

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84 84th Ann. Rept. Ent. Soc. Ont. (1953): 35-45, 1954.
85 *Canadian J. Agr. Sci.* 36: 81-94, 1956.
86 Defence Research Board of Canada, Suffield Rept. 176, 1953.
87 Defence Research Board of Canada, Suffield Tech. Paper 36, 1953.
88 *Agr. Inst. Rev.* 6 (4): 37-43, 1951.
89 *J. Physiol.* 132: 343-357, 1956.
90 *Nature* 175: 946, 1955.
91 *J. Agr. Food Chem.* 3: 56-61, 1955.
92 *Enzymologia* 17: 73-89, 1954.
93 *Biophys. Acta* 17: 294-296, 1955
94 *Nature* 172: 1004, 1953.
95 *J. Anim. Ecol.* 18: 1-35, 1949.

passionate reviews of this field, there are only four citations to Canadian work in a list of 152 references. It is natural that integrated studies of the whole control complex should be a late, rather than an early, development in any country. In order to have a sound basis, studies of this type require much preliminary work on the taxonomy and life-histories of both the phytophagous pest and its enemies, and on host preferences, distribution, genetics, physical ecology, sampling systems, etc. Another factor retarding the development of population dynamics, particularly before 1945, was the limitation in research staff in contrast to the wide variety of forest and crop conditions occurring across Canada. Outbreaks of native insects as well as the accidental introduction of several foreign species demanded much attention to surveys of distribution and damage and to immediate control measures. Until the past decade or so, Canadian entomologists were literally rushing from one outbreak to the next.

This section deals briefly with four early contributions, a number of factors promoting population work in more recent years, and some of the investigations that are now in progress. The work has been undertaken almost wholly by officers of the Canada Department of Agriculture.

Between 1912 and 1919, J. D. Tothill,[96] who had formerly been associated with the well-known United States entomologists H. S. Smith and W. F. Fiske, studied the population dynamics of the fall webworm, *Hyphantria cunea* (Drury). His intensive work was done in central New Brunswick, but he gathered supporting data in northern New Brunswick, Nova Scotia, and British Columbia. Two factors, parasites and birds, appeared to play the major role in the dynamics of this species and it is clear that Tothill was aware of the fundamental problems involved, including the density relationships. He showed that birds decreased in effectiveness as webworm populations reached a high level; parasitism, on the other hand, increased in intensity with the rise in host population and decreased very markedly as the host became scarce. This would be expected from Nicholson's theory, which was not published until some ten years later. Tothill devoted much of his paper to the biologies of the important parasites and one could wish that he had presented his population data and life tables in much greater detail. The fall webworm lends itself very well to population work and annual records of the type made by Tothill are now being resumed in New Brunswick.

Pioneer work on quantitative sampling methods and on population dynamics of soil-inhabiting insects was spearheaded by K. M. King[97] in Saskatchewan. In 1928, King and N. J. Atkinson[98] described important interrelations between parasites and disease affecting the abundance of the red-backed cutworm, *Euxoa ochrogaster* (Guen.). They conculded that disease is the most effective factor in reducing outbreaks of this pest, that high incidence of disease in one year results in a greater ratio of parasites to moths the next year, and that parasites influence population oscillations and reduce the rate of increase between outbreaks. In the 1930's King and his associates initiated several long-term quantitative investigations of wireworms and grasshoppers, the results of which have not been fully published to date.

The European corn borer, *Pyrausta nubilalis* (Hbn.), was studied rather intensively in Ontario from 1929 to 1936. In his detailed paper on this work, G. M. Stirrett[99] did not develop any general theory concerning the population

96 Canada Dept. Agr. Bull. 3, n.s., 1922.
97 *Ecol. Monogr.* 9: 270-286, 1939.
98 Ann. Ent. Soc. America 21: 167-188, 1928.
99 *Sci. Agr.* 18: 355-369, 462-484, 536-557, 568-585, 656-683, 1938.

dynamics of this species; rather, he was impressed by the multiplicity of factors contributing to mortality and by the fact that different factors were prominent in different years.

John Stanley, McGill University, is the only Canadian biologist who has made important contributions to mathematical theories concerning population growth. Working with populations of the confused flour beetle, *Tribolium confusum* Duv., under controlled laboratory conditions, he attempted a detailed analysis of all the factors affecting increase and derived a series of complicated equations for each stage in the development of the population. In the comparatively short period from the start of the cultures until the first egg had hatched, Stanley[100] recognized the action of no fewer than 14 factors, and these became represented in his subsequent calculations by a much greater number of mathematical symbols. This work indicates that the population growth of insects is a much more complex phenomenon than is represented by the simple assumptions underlying the exponential or logistic growth curves.

In more recent years, increased attention to intensive, long-term studies in population dynamics has been encouraged by several developments: 1. Greater awareness in Canada, as in other countries, of the need for a basic understanding of population dynamics. The high cost, temporary nature, and frequent failure of empirical control measures have served to emphasize this. 2. The establishment of permanent field centres where teams of research men may devote their full time to population dynamics over a period of years without the distraction of other problems. 3. The establishment of a co-ordinated, nation-wide forest insect survey. The annual records of this survey on the distribution and abundance of both phytophagous insects and their parasites should, over a period of years, contribute much to population dynamics. Even more important, however, is the fact that this development relieves many workers of survey responsibilities so that they are free for intensive investigations at permanent locations. 4. Creation of Science Service (Canada Department of Agriculture), which is doing much to improve the quality of both the work and the workers.

One of the most rapid advances during this recent period has been in bioclimatology. In a new approach based on the integration of field and laboratory observation, W. G. Wellington and his associates[101] have defined the reactions of the spruce budworm, *Choristoneura fumiferana* (Clem.), and of other species to light, temperature, and humidity. This information, aside from the interest of the technique, greatly facilitates the development of sound population procedures for the species concerned. A still more useful advance in this field is the development of the synoptic approach to studies of insects and climate. By this method, Wellington[102] was able to show that the three- to four-year periods preceding budworm outbreaks in central Canada were characterized by southward shifts in the circulation pattern which permitted polar air to predominate over the affected areas. This was attended by reduced precipitation and by the dry and clear air conditions most suitable for budworm development. The forest tent caterpillar, *Malacosoma disstria* Hbn., on the other hand, is favoured by the type of weather associated with humid air masses of tropical origin, and there is good evidence that its outbreaks are associated with the prevalence of such air masses. This evidence of a "climatic release" from natural control helps to explain the incidence of budworm outbreaks in both time and place, and should have a useful predictive value. Supporting

100 *Canadian J. Res.* 11: 728-732, 1934; *Ecology* 22: 23-37, 1941.
101 *Canadian Ent.* 80: 56-82A, 1948; 85: 297-310, 1953; 86: 207-222, 261-274, 1954.
102 *Meteorol. Monogr.* 2(8): 11-18, 1954; *Canadian Ent.* 86: 312-333, 1954.

evidence of climatic release for budworm outbreaks in New Brunswick is presented by D. O. Greenbank,[103] who is also investigating the possible mechanisms through which it may operate.

The application of chemical control measures can shed much incidental light on the population dynamics of insects. The long-term work of A. D. Pickett[104] and his associates on the phytophagous, parasitic, and predacious fauna of sprayed and unsprayed orchards in Nova Scotia is outstanding in this regard. Outbreaks of scale insects and mites, some of which had previously been unimportant, were found to be associated with the use of certain chemicals and this could be directly attributed to the effect of the chemicals on their predators. Apart from the consequent improvements and reductions in spraying schedules, this work, which is still in progress, contribues much information of value to the general field of population dynamics. It is notoriously difficult, for example, to assess the value of insect predators by ordinary methods, but here we have a technique that shows rather convincingly that certain predators are important regulatory factors for certain insects. Large-scale aerial spraying against the spruce budworm, as discussed by F. E. Webb,[105] is also providing valuable information, especially as regards moth dispersal and population dynamics following spraying.

The study of introduced species in the absence of the natural enemies of their original habitat is another rich source of information on population dynamics. Such introductions have been of particular concern in the Maritime Provinces and have impressed entomologists of that region with the importance of biotic factors of control. The work of R. E. Balch and his associates on the European spruce sawfly, *Diprion hercyniae* (Htg.), presents a clear-cut example of control achieved through the introduction of biotic agents. The sawfly had already reached outbreak proportions when its presence was discovered, and detailed population work showed that the existing mortality factors were incapable of preventing further increase and spread. The importation of European parasites was commenced at once and in 1938 a virus disease, apparently introduced with the parasites, brought about the collapse of the outbreak. After the population reached a low level, the introduced parasites became effective and are now the major regulating factor. The virus has retained its virulence, however, and can become effective again during relatively minor peaks in host abundance. Uninterrupted records on population and major control factors are now available for periods of 20 years on certain study plots but unfortunately no integrated account covering all aspects of population dynamics of this species is yet available in published form. Similar studies are in progress on the introduced species *Adelges piceae* (Ratz.), with particular reference to the importation of its predators, and on a number of other introduced pests.

The study of outbreaks of native species provides some information of interest. For example, a paper is in preparation covering three outbreaks of the black-headed budworm, *Acleris variana* (Fern.), one in Cape Breton Island, one in British Columbia, and one in New Brunswick, and shows that the factors involved in population collapse were rather distinctly different in each case. Work now in progress on this species at its endemic level should provide more valuable information, however, on its population dynamics.

Some the important theories about the natural control of insects are based on certain assumptions concerning the behaviour of a parasite in relation to the density of its host. Studies designed to elucidate this behaviour can therefore

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103 *Canadian J. Zool.*, in press.
104 *Canadian Ent.* 85: 472-478, 1953.
105 *For. Chron.* 31: 342-352, 1955.

make important contributions to population dynamics. Work in progress by T. Burnett[106] on controlled populations of the sawfly *Neodiprion sertifer* (Geoff.) and its parasite *Dahlbominus fuscipennis* (Zett.) is providing significant data on the effects of temperature, host density, and parasite density on the rate of increase of the parasite. L. G. Monteith,[107] in the first of a series of studies on host selection by the parasite *Drino bohemica* Mesn., shows the importance of the foliage on which the host insect is feeding and of conditioning to the olfactory responses of the parasite. K. Graham and M. L. Prebble[108] studied the distribution of the eggs of *Blastothrix sericea* (Dalm.) in natural populations of *Eulecanium coryli* (L.). C. A. Miller[109] is devoting particular attention to the quantitative assessment of parasitism in natural populations over an extended period of years. The information on parasite and predator behaviour provided by these studies, and by others, will undoubtedly be pertinent to the interpretation of population phenomena.

Population dynamics, by its very nature, requires that we should be able to measure changes in population and, preferably, that we should be able to do this within known limits of statistical confidence. The attention of Canadian entomologists to reliable sampling procedures in recent years is a very encouraging development in population dynamics in this country. Working mainly with the European corn borer and the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), G. Beall improved techniques for measuring the populations of agricultural insects; also, his modification[110] of the hyperbolic sine transformation for the stabilization of variance is the most precise transformation for insect population data that has been developed to date. R. H. E. Bradley[111] has suggested improvements in the measurement of aphid populations on potato plants, based on a study of the distribution of the various species on the plant. The derivation of definite conclusions on the dynamics of the European spruce sawfly, described above, was greatly aided by the development early in the program of a reliable cocoon sampling method (M. L. Prebble[112]). In the past five years or so, Canadian biologists have made outstanding progress with the difficult problems involved in the population measurement of defoliating insects in the forest and it is not possible here to give complete references to these interesting contributions. R. F. Morris[113] has summarized the general principles involved, while developing a detailed sampling design for the spruce budworm.

Forest entomologists in Canada have been greatly impressed by the role of stand factors in population dynamics, and hence with the possibilities of cultural control as outlined by R. E. Balch.[114] Outbreaks of the spruce budworm, for example, appear first in certain types of susceptible forests even when climatic release may be favourable to population development in other types. Intensive, long-term studies by a team of workers on the Green River watershed in New Brunswick are designed to elucidate the population dynamics of the budworm and other defoliators of balsam fir, with particular regard to different silvicultural environments (R. F. Morris *et al.*[115]). The approach to this work is the development of complete life tables for the insect during successive generations in various types of forest stands. The relation of both larval and moth dispersal to stand density and isolation is proving to be extremely important in population

106 *Physiol. Zool.* 27: 239-248, 1954.
107 *Canadian Ent.* 87: 509-529, 1955.
108 *Canadian Ent.* 85: 153-181, 1953.
109 *Canadian J. Zool* 33: 5-17, 1955.
110 *Biometrika* 32: 243-262, 1942.
111 *Canadian Ent.* 84: 93-102, 1952.
112 Trans. Roy. Soc. Canada, 3rd Ser., 37 (Sec. 5): 93-126, 1943.
113 *Canadian J. Zool.* 33: 225-294, 1955.
114 65th Ann. Rept. Ent. Soc. Ont. (1934): 43-49, 1935.
115 *Canadian J. Zool.* 32: 283-301, 1954.

dynamics. In view of these relationships, forest entomologists are likely to be impatient with attempts to develop comprehensive population theories from work on confined laboratory populations of insects. Life table methods are also being applied to the larch sawfly, *Pristiphora erichsonii* (Htg.), in Manitoba and the lodgepole needle miner, *Recurvaria* sp., in Alberta. The larch sawfly program is also of particular interest to population students for another reason. Its major parasite, the introduced species *Mesoleius tenthredinis* Morley, has suffered a marked decline in effectiveness in central Canada through encapsulation of its eggs by the host (Muldrew[116]), whereas in British Columbia and the Maritime Provinces the parasite appears to be as effective as ever. This may be an example of an evolutionary change which, like the development of resistance to insecticides, confers an advantage to the pest species.

No important contribution to population theory has been made recently by Canadian entomologists. The major works of W. R. Thompson were published while he was working in or for other countries. Glen[117] has presented a brief review of population theory in relation to some current Canadian programs, and his conclusions are notable for their objectivity. This paucity of references is due not to lack of interest among Canadian entomologists in population theory but rather to an objective tendency to await the accumulation of more adequate empirical data before entering this perplexing field.

Most of the important insects under study in Canada have only one generation a year and it is a healthful sign that the workers concerned recognize that long-term work is necessary and that worth-while conclusions on population dynamics are not likely to be reached by studying only two or three generations. The relative stability of the forest environment as contrasted to that of annual crops, and the existence of virgin forests in many parts of Canada, present an unparalleled opportunity for the study of population dynamics under natural conditions. It is predicted that Canadian biologists in the decades immediately ahead will make important contributions and that these will serve to support or refute existing theories or perhaps to bridge the gaps between those theories which appear to differ more in emphasis and semantics than in substance.

Field Crop and Vegetable Insects

Insects affecting field crops and vegetables were often mentioned in the writings of the pioneer naturalists of the late 1800's, frequently only as interesting captures for their collections. The first important publications on economic entomology appeared in 1857: H. Y. Hind's "Essay on the Insects and Diseases Injurious to the Wheat Crop" and Lèon Provancher's pamphlet on the same subject. In 1872, C. J. S. Bethune wrote on "Insects Affecting the Wheat Crop" and "Insects Affecting the Cabbage" and E. B. Reed reported on "Insects Attacking the Cucumber, Melon, Pumpkin and Squash" and on "Insects Injurious to the Potato". Also in 1872, J. Pettit[118] published the life-history of the wheat wireworm, *Agriotes mancus* (Say), an insect causing such severe losses to wheat in eastern Canada that he reared it to determine the species.

In general, developments in Canada have paralleled those in the United States, with whom we have many problems in common. The early Canadian writings were based largely on local observation and on control recommendations issuing from the United States and Great Britain. Limited experimental work was attempted in the late 19th and early 20th centuries. However, field research did not begin in earnest until after 1911, when federal and provincial laboratories

116 *Canadian J. Zool.* 31: 313-332, 1953.
117 *J. Econ. Ent.* 47: 398-405, 1954.
118 *Canadian Ent.* 4: 3-6, 1872.

were established. Even then emphasis was on relatively simple field experiments, which sufficed in many cases. But as the easy problems were solved, the research program became more and more basic in character and the methods correspondingly more precise. Today, work on field crop and vegetable insects forms the largest section of agricultural entomology in Canada.

Research in the Federal and Provincial Services

From 1884 to 1908, when James Fletcher was the Dominion Entomologist, research on insects affecting field and vegetable crops was largely empirical. Nevertheless, much useful work was done, as is revealed in Fletcher's extensive bulletin of 1905, "Insects Injurious to Grain and Fodder Crops, Root Crops and Vegetables", which was an excellent paper in its day and contained original observations, many quotations from United States writers and Canadian growers, and control recommendations taken largely from current literature. In 1912, the second Dominion Entomologist, C. G. Hewitt, expanded research on field crop and vegetable insects by appointing two field officers, one in southwestern Ontario and the other in British Columbia. Relevant expansion continued until by 1919 field laboratories were functioning in all provinces except Prince Edward Island. From that time on, the great bulk of such research has been conducted by officers of the Canada Department of Agriculture. In 1956, 18 laboratories, extending from St. John's, Nfld., to Victoria, B.C., and a staff of 195, including 90 full-time professional entomologists, are engaged in this work.

In 1914, Hewitt placed his senior assistant, Arthur Gibson, in charge of vegetable insect investigations and in 1915 increased the responsibility to all field crop and garden insects. Thus began the Field Crop Insect Unit, known before 1938 as the Division of Field Crop and Garden Insects. Gibson was followed in this office in 1921 by R. C. Treherne, who improved the organization and coordination of the work of the field laboratories. Treherne died in 1923 and was succeeded in 1925 by H. G. Crawford, who in turn was succeeded in 1944 by H. L. Seamans.

Throughout the development of this work, investigations have centred on species of major economic importance. Studies of life- and seasonal-history were gradually augmented by studies on ecology, behaviour, natural control agents, food plants, insect transmission of plant viruses, cultural and chemical control, and assessment of economic importance. Ecological investigations have included the reactions of species to temperature, moisture, light, soil type, weather, climate, and cultural programs; and the objectives have been expanded to include prediction of outbreaks as well as control. Special projects have been initiated as required on such features as winter-hardiness, diapause, and nutrition. The possibility of developing resistant host plants has been studied since 1934, partly by field selection of plants that appeared to be resistant and partly by definite breeding programs. The co-operation of plant breeders, geneticists, plant physiologists, and biochemists was enlisted to assist the insect physiologists and nutritionists. The development of organic insecticides, starting with DDT in 1944, and the conflicting results obtained, indicated the need for standardizing of materials, application procedures, and methods of assessment. The toxicologist thus became important in the modern control program, especially in formulating insecticides and in determining their effectiveness, phytotoxicity, and possible hazard to the health of man and animals. Where the same species occurred in widely different climatic areas or soil types, co-ordinated research programs were frequently developed to compare life- and seasonal-histories, behaviour, and the effectiveness of control.

The development of research on field crop and vegetable insects by educational institutions and provincial governments has followed much the same pattern as in the federal service, though it has been more restricted in scope. In many provinces, the universities and colleges have contributed considerably through direction and supervision of research of graduate students. However, many of these students have been employees at federal government laboratories and often have continued part of their official research for thesis purposes. In this way, the work of universities and of the federal service have become closely associated. Apart from such contributions, research in Saskatchewan has been confined largely to the study by J. G. Rempel of the embryological development of the bertha armyworm, *Mamestra configurata* Wlk.; that in Alberta, primarily to the work of E. H. Strickland on the biology of wireworms and the control of grasshoppers; and that in the Atlantic provinces to certain life-history and control experiments undertaken at the Nova Scotia Agricultural College at Truro. In the other provinces, more extensive field researches have been developed by officers of the departments of agriculture and staffs at agricultural colleges, often working in close collaboration.

In Ontario, J. Hoyes Panton, the first lecturer in entomology at the Ontario Agricultural College, conducted investigations as early as 1885 on the life-histories and behaviour of injurious insects. His successors also took a lively interest in economic entomology, centring their field researches in southwestern Ontario and studying particularly pests of legumes and, more recently, root maggots. J. Dearness and J. D. Detwiler at the University of Western Ontario were also active in this field, the latter doing considerable work on insects attacking legume forage crops.

In Quebec, significant experimental work was begun by William Lochhead, who resigned from the Ontario Agricultural College in 1905 and joined the staff of Macdonald College. He organized instruction in entomology in 1907 and directed investigations on life-histories, habits, and control of insects affecting field crops and vegetables. J. M. Swaine and E. M. DuPorte also participated in some of the early work. In 1913 the Quebec Department of Agriculture established the position of Provincial Entomologist with headquarters at Quebec City. L'Abbé V. A. Huard was the first incumbent. He was succeeded by G. Maheux in 1916, who was succeeded by G. Gauthier in 1950. Although the Provincial Entomologist and his staff are primarily responsible for extension and service work, they have also conducted research on life-histories, habits, and control of insects attacking field crops and vegetables. A limited amount of research on economic insects has also been done at the Provincial Agricultural School at Oka, particularly under the direction of the late Father Leopold.

H. McKellar, Chief Clerk in the Manitoba Department of Agriculture in the late 1890's, and later Deputy Minister of Agriculture, conducted simple experiments in the control of grasshoppers, cutworms, and the hessian fly, *Phytophaga destructor* (Say), using Fletcher's recommendations. In 1918, A. V. Mitchener was appointed to the Entomology staff at the Manitoba Agricultural College. Thereafter the College gradually took responsibility for the entomological activities formerly conducted by the provincial department, except control campaigns. Mitchener and his staff developed an extensive program on life-histories, behaviour, and control of insects affecting field crops and vegetables, particularly in the Red River Valley and the vicinity of Winnipeg. A. J. Thorsteinson, who succeeded Mitchener in 1954 as Head of the Department of Entomology, is conducting research on insect nutrition and feeding stimulants, with particular reference to field crop pests.

The development of research on field crop and vegetable insects by the government of British Columbia began with the establishment of the Provincial Board of Horticulture in 1892. Some of the horticultural inspectors conducted experiments on the control of vegetable insects. In 1918, M. H. Ruhmann, of the Provincial Entomologist's staff, began investigations on life-histories and control of the onion maggot and cutworms affecting vegetables, and E. R. Buckell on grasshoppers affecting the cattle ranges. Since 1918, however, all research in British Columbia on field crop and vegetable insects has been conducted by the federal service.

Research on Major Problems

Hundreds of species of insects attack field and vegetable crops in Canada and many have been investigated intensively. However, this discussion is confined largely to summary statements of the major pests or groups of pests and the beneficial forms that pollinate legumes.

Grasshoppers

The earliest report of grasshoppers in Canada[119a] concerned an invasion in 1818 by what was probably the Rocky Mountain grasshopper, *Melanoplus spretus* (Walsh), which destroyed all the crops in the new Selkirk settlement in the Red River Valley of Manitoba. Since then, outbreaks have occurred in the West in 1830, 1842, 1856, 1863, 1873-1876 (Rocky Mountain grasshopper), 1893, 1899-1903, 1919-1923, and, worst of all, 1930-1951. Outbreaks of somewhat less importance occurred in Eastern Canada in 1893, 1902, 1914-1915, 1920, and 1949. Although there are many species of grasshoppers in Canada, the large outbreaks are usually caused by four or five common forms.

Canadian research on grasshoppers started during the 1899-1903 outbreak, when Norman Criddle, a gifted naturalist, observer, and artist, studied the life-history, behaviour, habits, and natural enemies of the species found on his family farm at Aweme, Man. In 1901 he developed the "Criddle mixture", a bait made from fresh horse droppings, salt, and paris green, to replace the expensive poisoned bran bait that had first been used in California in 1885. In 1903, Fletcher sent Criddle a culture of an entomophagous fungus secured from the United States, but it failed to control the grasshoppers.

During the 1919-1923 outbreak, Criddle, then a field officer in the Entomological Branch, determined the temperatures at which grasshoppers fed and recommended that bait be spread only at temperatures between 68 and 90°F. for maximum efficiency. E. R. Buckell and R. C. Treherne found that *Cammula pellucida* (Scudd.), the species feeding on range grasses in British Columbia, preferred to deposit its eggs on overgrazed areas. Good control was obtained by range management involving rotation of grazing and the poisoning of grasshoppers on localized egg beds, before they dispersed. It was during this outbreak that the provincial governments of the western provinces took over the responsibility for grasshopper control campaigns.

In the outbreak of 1930 to 1951, quantitative methods of survey were developed and co-ordinated with those in the United States, and annual forecast maps were prepared for each of the three prairie provinces. Cheaper and more effective baits and methods of spreading them were discovered. By 1941, the standard Canadian bait consisted of 13 parts of sawdust and 1 part of cheap flour[119b] poisoned with sodium arsenite or sodium fluosilicate. It was recommended at 10 to 20 pounds per acre and was usually applied by hand. With the advent of the new and more toxic organic insecticides in 1945, experiments with

[119a] North Dakota History 16(3): 144, 1949.
[119b] *Sci. Agr.* 24: 332-340, 1944.

sprays and dusts were undertaken. As a result, baiting has now been largely replaced by spraying. Good results have been obtained, for example, by using aircraft to apply dieldrin at two ounces per acre.

The marked difference found from year to year in the hatching dates of the same species of grasshopper has been explained through a study of the embryological development[119c] and diapause in the overwintering eggs. It is now possible to predict whether hatching will be late or early. Much information has been accumulated on the various factors that bring about outbreaks or cause them to decline. Recent emphasis in this work has been on the effect of food plants,[119d] weather conditions, parasites, and diseases.

Cutworms and Armyworms

Research on pest species of cutworms has been conducted in every province. Studies on oviposition revealed that not all species deposit eggs on vegetation, as stated in early writings, but that those that feed on grasses or annual plants and spend the winter in the egg or larval stage usually deposit their eggs in the soil; those that feed on perennials or that oviposit during the spring or summer usually deposit their eggs on vegetation.

Armyworm—The armyworm, *Pseudaletia unipuncta* (Haw.), appears at irregular intervals in enormous numbers, feeding on grains, grasses, and forage crops, and moves in armies. Severe outbreaks have occurred in 1896, 1914, 1929, and 1954. Panton[120] published an extensive report on the outbreak of 1896 and showed there were two complete generations a year in Ontario, the larvae and occasionally the moths of the third generation overwintering. He determined the food plants, parasites, and predators of the species in Ontario. No extensive outbreak of the armyworm has lasted more than one season and little has been added to Panton's findings.

Army cutworm—The army cutworm, *Chorizagrotis auxiliaris* (Grote), occurs sporadically in the Prairie Provinces. When abundant, the larvae move in armies, destroying vegetation as they march. Strickland[121] determined the life- and seasonal-histories, parasites, predators, diseases, and habits of larvae and adults, and used bundles of stink weed (*Thlaspe arvense*) poisoned with paris green as a control measure. H. L. Seamans[122] determined the weather relationships and showed that fall precipitation could be used in forecasting outbreaks. In 1955 an outbreak in Saskatchewan was controlled by spraying with dieldrin.

Red-backed cutworm—The red-backed cutworm, *Euxoa ochrogaster* (Guen.), occurs in every province and is mentioned in the earliest literature as attacking all field and vegetable crops. Gibson recorded the life-history in Ontario and K. M. King[123] showed that in the Prairie Provinces it occurred mainly in the parkland areas. H. McDonald revealed that sprays of dieldrin or aldrin were more effective than poisoned bait in Saskatchewan; and R. H. Handford found that good control could be secured in British Columbia by introducing the insecticide into the sprinkler irrigation system in market gardens.

Pale western cutworm—The pale western cutworm, *Agrotis orthogonia* Morr., occurs in the drier areas of Alberta and Saskatchewan and is probably the most destructive of the cutworms. It first appeared in Alberta in 1911, causing serious losses to wheat. Strickland found poisoned baits ineffective. Seamans,[124] in 1923, developed a method of forecasting outbreaks based on

119c *Canadian Ent.* 80: 83-88, 1948.
119d *Canadian Ent.* 84: 113-117, 1952.
120 27th Ann. Rept. Ent. Soc. Ont. (1896): 44-51, 1897.
121 Canada Dept. Agr., Ent. Branch Bull. 13, 1916.
122 58th Ann. Rept. Ent. Soc. Ont. (1927): 56-85, 1928.
123 Canada Dept. Agr., Ent. Branch Pam. 69, 1927.
124 *Canadian Ent.* 55: 51-53, 1923.

weather conditions. Investigations showed that survival, length of larval life, fecundity of females, viability of eggs, and survival of second-generation larvae varied greatly with different food plants. Seamans and P. J. G. Rock developed a cultural practice that starved the larvae in the spring; and L. A. Jacobson has shown that dieldrin sprayed on the soil surface provides an effective control.

Tobacco cutworms—Cutworms of several species feed on tobacco plants soon after they are set out in the field, cutting the stems at or just below the soil surface. D. A. Arnott and A. A. Wood, in southwestren Ontario, found that poisoned bran bait, scattered on the surface of the field a day or two before tobacco plants were set out, was an effective control. However, the use of some of the organic insecticides in the planting water has been found even more satisfactory.

Wireworms

There are more than 25 species of wireworms of economic importance in Canada. They occur in every province and are serious pests of cereals, root crops, potatoes, and tobacco. The life-histories of many are complicated, taking from one to ten years to complete. Through Canadian research, these pests have been brought under a high degree of control, first by cultural practices and more recently by use of the newer insecticides applied as seed dressings or as general soil treatments. Supplementary investigations have been concerned with food plants and internal anatomy in relation to development and reproduction, and with toxicology and temperature and moisture preferenda in relation to improved use of chemicals for control.

After Pettit published in 1872 on the life-history of *Agriotes mancus*, little was done in wireworm research in Canada until the 1920's, when K. M. King in Saskatchewan undertook investigations on the prairie grain wireworm, *Ctenicera aeripennis destructor* Brown. He showed that the old recommendations for control such as seed treatments with kerosene, turpentine, and arsenicals, or soil applications of salt, lime, and similar chemicals, were useless, too expensive, or phytotoxic. He also introduced quantitative sampling procedures into the research program on soil-inhabiting insects. In the 1930's, King, R. Glen, H. McMahon, and W. B. Fox conducted large-scale field experiments[125] from which was developed a control program based on cultural practices with emphasis on proper methods of summer-fallowing to reduce infestations gradually and proper methods of seeding to protect the grain crop at its most vulnerable stage. This ecological approach demanded accurate recognition of species in the larval stage and Glen, King, and Arnason ultimately determined characters for the separation of all species known to be of economic importance.[126]

In the late 1940's, also in Saskatchewan, A. P. Arnason with the assistance of W. B. Fox pioneered investigations on soil and seed treatments with BHC and obtained an effective wireworm control.[127] Further work showed that chlordane, aldrin, dieldrin, and heptachlor as soil or seed treatments all gave satisfactory results. The work in the Prairie Provinces is being continued under the direction of R. H. Burrage, Saskatoon. In southwestern Ontario, J. A. Begg has studied *Limonius agonus* (Say), which attacks tobacco in the area, and has developed an excellent control by using BHC or lindane in the planting water. King and A. T. S. Wilkinson, investigating a mixed wireworm population including *Limonius* spp. attacking vegetable crops in British Columbia, have found dieldrin, aldrin, and lindane effective when worked into the soil. In Nova Scotia, C. J. S.

125 *Sci. Agr.* 13: 646-652, 1933.
126 *Canadian J. Res.*, D, 21: 358-387, 1943.
127 Canada Dept. Agr., Div. Ent. Processed Pub. 111, 1948.

Fox, working with a number of noxious forms including three European species of *Agriotes* that injure pasture and hay meadows, has obtained effective control with surface applications of chlordane or aldrin.

White Grubs

Investigations of white grubs, *Phyllophaga* spp., began in 1914 with Criddle in Manitoba and H. F. Hudson in Ontario. They studied the life-histories and habits of the species occurring in their areas. Both found their species to have three-year life-cycles and Criddle observed that deep ploughing in the fall or spring was ineffective because the larvae and beetles burrowed below the plough-line in the autumn. In the 1930's, G. H. Hammond[128] showed that in Quebec and Ontario the adults occurred in different areas in different years; he designated the broods as A, B, and C and showed that there was virtually no overlapping of broods within a given area. Thus he was able to forecast when major flights of beetles would take place in any locality. Careful studies on life-history and behaviour showed that the beetles always lay eggs in sod or soddy patches of weeds in cultivated fields and that the lighter soils are more heavily infested than the heavier ones. From his earlier work, Hammond devised a multiple-disking control method which greatly reduced the numbers of grubs in the soil, developed effective crop rotations, and recommended the dusting of sulphur on the surface of sod to repel the beetles seeking oviposition sites. More recently, emphasis has been on the use of the new organic insecticides. BHC, heptachlor, and dieldrin sprayed on the surface of pastures kill beetles emerging from the soil and those returning to the sod for oviposition. The treatment of such lands with BHC also destroys the grubs in the soil and has kept land free of the pest for seven years. Heptachlor and dieldrin are also effective against the grubs but have not been used long enough to determine their residual effectiveness.

In Quebec, Maheux and Gauthier and his associates conducted investigations on white grubs and recommended cultural practices to destroy the pupae.

Wheat Stem Sawfly

The wheat stem sawfly, *Cephus cinctus* Nort., occurs in the prairies from southwestern Manitoba to the foothills in western Alberta. It is one of the most serious pests of wheat in Canada, annual damage having been estimated as high as fifty million bushels. Since this pest spends its whole life, with the exception of a few days, inside the stem of the wheat plant the possibilities for effective control measures are limited.

Fletcher first reported the wheat stem sawfly from Manitoba in 1896. Criddle[129] worked out its life-history and habits in that province and recommended that as durum wheat seemed to be resistant to attack losses could be avoided by growing it in preference to susceptible varieties. He also found that the sawfly oviposited in brome grass, *Bromus inermis*, and in oats, but the larvae failed to mature. Hence, these crops were recommended as traps.

In the late 1920's intensive studies on the behaviour, ecology, and control of the sawfly were begun by Seamans at Lethbridge for the Prairie Provinces and continued subsequently by his associates C. W. Farstad and N. D. Holmes.[130] Ploughing of infested stubble land retarded but did not prevent the flies from emerging, unless a mouldboard plough was used and followed by a packer. Traps of brome grass or early-seeded wheat, cut for hay about July 10, were helpful in reducing infestations. Much information has been gathered on such related features as host plants, effect of crop variety on sex ratio and fecundity, and

128 61st Ann. Rept. Ent. Soc. Ont. (1930): 69-73, 1931.
129 Canada Dept. Agr., Ent. Branch Bull. 11, 16-23, 1915.
130 *Canadian Ent.* 86: 159-167, 1954.

occurrence of biotypes within the species. Seamans[131] also published on the climatology of the sawfly and mapped the possible distribution of the species in Canada.

In 1937, when the spring and early summer were unusually dry and hot in Saskatchewan, Farstad found that the overwintered larvae in the wheat stubble did not pupate but remained for a second season in their hibernacula. This phenomenon was investigated by R. W. Salt, Lethbridge, who found that temperature and moisture acting together were required to break the larval diapause. Thus a very dry year, when there is virtually no wheat crop, may be followed by a more severe infestation than may occur after a normal season.

Co-operative investigations by Farstad and A. W. Platt of the Canada Experimental Farms Service resulted in the development of a resistant variety of hard spring wheat, Rescue, which is now grown over much of the sawfly-infested area of Canada and the United States. A second resistant wheat, Chinook, has been developed by Ruby I. Larson, Lethbridge, but its improved milling qualities are offset by its somewhat inferior resistance to the sawfly.

European Corn Borer

The European corn borer, *Pyrausta nubilalis* (Hbn.), was first found in Canada near Welland, Ont., in 1920. It spread rapidly, reaching southern Quebec in 1926, New Brunswick in 1928, Nova Scotia in 1929, and Manitoba and Saskatchewan in 1949.

The first investigations in Canada were conducted jointly by officers of the federal government and of the governments of Ontario and Quebec. H. G. Crawford, working with G. J. Spencer of the Ontario Department of Agriculture, determined that the borer had one generation per year but that pupation occurred occasionally in the summer, indicating that two generations were possible. In 1931, L. Caesar and R. W. Thompson of the Ontario department recorded a small second generation. H. B. Wressell,[132] Entomology Laboratory, Chatham, Ont., showed that since 1941 the percentage of borers of the multivotine strain has increased in southwestern Ontario and now exceeds 70 per cent. In Quebec and the Maritime Provinces, the species is univoltine but in Manitoba and Saskatchewan the multivotine strain is increasing. The latter attacks a wide range of plants, sweet peppers and late canning corn being severely damaged. Many of the native weeds harbour over-wintering larvae of the second generation and may form important foci of infestations.

G. M. Stirrett and his associates at Chatham showed that dry weather at the time of hatching retarded borer establishment in the corn. They assessed the value of "clean-up campaigns" where growers were compelled by law to plough under, burn, or in other ways destroy corn refuse in the fields, and showed that the fluctuations in abundance of the pest were caused by weather and not by sanitary measures.

Recent experiments with hybrid corn disclosed that certain varieties are resistant to the borer and may provide an effective means of control. Some varieties escape injury because they are resistant to larval penetration and others because they are strong-stemmed and do not break over when attacked. Chemical control is achieved by spraying or dusting with DDT or ryania when the eggs begin to hatch.

Forage Crop Insects

Legume forage crops, particularly alfalfa and clover, including sweet clover,

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131 *Sci. Agr.* 25: 432-457, 1945.
132 84th Ann. Rept. Ent. Soc. Ont. (1953): 45-47, 1954.

are important in Canadian agriculture as feed for livestock and as soil-improvement inclusions in crop rotations. Alfalfa and clover seed also provide important cash crops in many areas. The majority of the species that attack the seed have been determined and effective controls devised. Present emphasis is on pollinating species.

H. A. McMahon, G. A. Hobbs, and T. Cole, Entomology Division officers in the Prairie Provinces, and D. H. Pengelly of the Ontario Agricultural College, have determined the species of wild bees that are the most important pollinators of alfalfa in their regions. They[133] have found honey bees to be of little importance in seed production in Canada to date. Hobbs has shown that cross-pollination produces larger yields of alfalfa seed, that bumble bees and leaf-cutter bees will cross-pollinate alfalfa, but the former prefer red clover and will not visit alfalfa blossoms if there is red clover in the vicinity whereas the latter prefer alfalfa. The problem is being studied under both dry and irrigated conditions of farming. Investigations are continuing on seasonal abundance, habits of nesting, feeding, and brood care with a view to assessing the value of each species in each important region; on managing seed fields to get maximum efficiency from the native pollinators; and on means of increasing the population of wild bees.

Aphids

Research has been conducted on only a few of the many species of aphids that attack field and vegetable crops. Particular attention has been given to those affecting potatoes, peas, and tobacco. Serious infestations in grain crops have occurred, especially in recent years, but excellent control has been obtained by timely application of malathion.

Four species of aphids attack potatoes in the Maritime Provinces, at least one being capable of transmitting virus diseases. The life-history, including the alternate hosts, of each species has been determined and control experiments have shown that at least one species is resistant to DDT. A study of aphid habits and feeding mechanisms has been undertaken to clarify the problems involved. Mrs. J. B. Adams and J. W. McAllan have found two salivary enzymes in the green peach aphid, *Myzus persicae* (Sulz.), that digest cellulose, suggesting that aphids "dissolve" their way into plant tissues instead of forcing the stylets in by pressure.

Investigations on the pea aphid, *Macrosiphum pisi* (Harris), are centred at the Science Service Laboratory at St. Jean, Que. The long-term objective is to define the nature of plant resistance to aphid attack. J. B. Maltais has developed a variety of pea that is resistant to colonization of the aphid; and he and J. L. Auclair have found resistance to be correlated with the kinds and amounts of amino acids and carbohydrates present in the plant. An effort is being made to rear the species on a chemically defined diet so that resistance can be related directly to nutritional requirements of the insect.

Further research on aphids is reported on page under "Insects as Vectors of Plant Viruses".

Root Maggots

Root maggots attacking onions, carrots, and crucifers constitute one of the major problems of vegetable production in Canada. Investigations on life-histories and control produced conflicting results in different areas and little progress was made until 1949, when A. R. Brooks,[134] Saskatoon, made a critical study of the Canadian species. He found that at least five species attacked crucifers and three attacked onions, and that all species were not present in all parts of the country.

133 *Canadian J. Agr. Sci.* 35: 422-432, 1955.
134 *Canadian Ent.* 83: 109-120, 1951.

Identification of the species occurring in each area and knowledge of the seasonal-histories and numbers of generations per year made it possible to develop effective control measures. These consist of seed treatments with aldrin, dieldrin, or heptachlor; and soil treatments[135] by broadcasting the insecticide on the soil and working it in shallowly or by applying the insecticide in a band, working it into the soil, and seeding along the centre of the band. Seed treatments are effective for control of the seed-corn maggot, *Hylemya cilicrura* (Rond.), which attacks corn, beans, peas, and cucumbers; and soil treatments for the carrot rust fly, *Psila rosae* (F.). W. G. Friend, Ottawa, has reared the onion maggot, *Hylemya antiqua* (Mg.), aseptically on a chemically defined diet and has determined the gross nutritional requirements of the species.

Other Research

The Canadian work on field crop and garden insects is much more diverse than the foregoing abbreviated account indicates. Many other species have been studied and several other lines of approach have been taken. For example, annual surveys of abundance and prediction of outbreaks have been made regularly for grasshoppers and the pale western cutworm; radio-active tracers have been used to study the vertical and lateral movements of wireworms[136] and cutworms in the soil, and the rate and pattern of dispersal of grasshopper nymphs; chromosome patterns have been examined in closely related species of aphids in a search for supplementary identifying characters; low temperatures and cold-hardiness have been related to winter mortality, survival, and development in the wheat stem sawfly, cutworms, and grasshopper eggs; a number of species and varieties of *Solanum* from various parts of the world have been screened for resistance to the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), and to aphids attacking potatoes; phytotoxicity tests have been made on a number of plants, particularly on varieties of cucumber[137] and tomato; and serological techniques have been employed in assessing the insect predators of wireworms.

Fruit Insects

The fruit industry in Canada has achieved its present status largely because effective measures for insect and disease control have been provided. No other branch of our agriculture is so dependent for its survival on entomological investigation and knowledge. This fact has become particularly evident during the present century, although it was vaguely appreciated 85 years ago when measures for the control of fruit insect pests were first coming into use. The rise of pest insects from relative unimportance to serious economic status coincides with the rapid expansion of commercial orchard acreage during the latter part of the nineteenth century and the first decade or two of the twentieth. The number and abundance of pests, many of them introduced, increased steadily during this period until in recent times complex and expensive programs have been necessary for the protection of the crop. This situation has developed even though more potent insecticides and more efficient spraying and dusting equipment are available than in the pioneering days of orchard entomology. This has led to a restudy of the problem on a broad ecological basis that may lead to some reduction in production costs with little or no loss in protection, by avoiding materials and methods that reduce the effectiveness of natural agencies in controlling pest species.

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135 *J. Econ. Ent.* 74: 607-615, 1954.
136 81st Ann. Rept. Ent. Soc. Ont. (1950): 7-15, 1951.
137 *Canadian Ent.* 82: 102-111, 1950.

Developments in Federal and Provincial Services

Orchard entomology in Canada had its beginnings 85 years ago with the publication in 1871 of the reports[138] on insects affecting the apple, grape, and plum by C. J. S. Bethune, W. E. Saunders, and E. B. Reed. These reports provided the first reliable information on fruit insects and their control in Canada. *Insects Injurious to Fruits*, by Saunders, first published in 1883 and revised in 1900, was the standard reference on fruit insects in North America for almost a third of a century.

Developments in Canada have been similar to those in the United States. At first they were the result of field observation and simple experimentation by fruit growers and the part-time efforts of Saunders, James Fletcher, Bethune, W. Lochhead, and a few others. Control measures, which at first were based on recommendations obtained from the United States and Great Britain, were founded largely on local experience after the beginning of the century. However, it was not until federal and a few provincial laboratories were established between 1911 and 1917 in the four principal fruit-growing regions that research was placed on a permanent basis. For some years simple field experiments and observations were sufficient for the solution of many problems. But, as problems grew more difficult, more comprehensive and detailed studies were undertaken. In recent years, emphasis has been on testing insecticides and acaricides, improving spray formulations and application equipment, and ecology of the orchard fauna with special attention to effects of chemicals on species abundance and interrelations.

Participation by the Canada Department of Agriculture in work on fruit insects began with the appointment in 1884 of Fletcher as Dominion Entomologist, but for more than a quarter of a century neither staff nor facilities were provided for field investigation. Yet Fletcher collected and published in his reports a great deal of information about fruit insects from all parts of Canada, and he was a tremendous influence in getting growers to do something about them. John Craig, Dominion Horticulturist, conducted the first spray experiments between 1890 and 1895 and with Fletcher in 1895 published the first spray calendar in Canada for insects and diseases of apple and cherry. Another important event in this period was the enactment of the San José Scale Act in 1898, the first federal legislation on insects, which prohibited the importation of nursery stock from countries infested by the scale and which was the forerunner of the more comprehensive Destructive Insect and Pest Act of 1910. Enforcement of these acts and similar provincial legislation delayed the introduction and retarded the spread of foreign and domestic pests.

The first laboratory for study of fruit insects was established in 1911 by C. G. Hewitt, the second Dominion Entomologist, at Vineland Station, Ont., with R. C. Treherne in charge. When Treherne was moved to British Columbia later in the year, he was succeeded by W. A. Ross. Between 1911 and 1919 six other laboratories were established, one in each of Nova Scotia (1912), New Brunswick (1917), and Quebec (1912) and three in British Columbia (1911, 1915, and 1917). Other laboratories were added in subsequent years until today fruit insects are studied at ten laboratories; these are mostly well equipped, and have a total staff of about 80, of which 45 are research entomologists.

The present laboratories, the officers-in-charge and the number of research officers, and the principal research problems are as follows:—

Kentville, N.S.: A. D. Pickett and 10 research officers; life-histories, habits,

138 1st Ann. Rept. Ent. Soc. Ont. (1870): 68-93, 94-117, 118-128, 1871.

ecology, and control of apple insects; development of control programs designed to harmonize chemical and biological control in apple orchards.

Fredericton, N.B.: C. W. Maxwell and three research officers; life-histories, habits, ecology, and control of small-fruit insects, including blueberry and cranberry insects.

St. Jean, Que.: A. A. Beaulieu and three research officers; life-histories, habits, ecology, and control of apple insects.

Vineland Station, Ont.: G. G. Dustan and seven research officers; life-histories, habits, ecology, and control of insects affecting tree fruits and grapes; vectors of stone-fruit viruses; development of control programs designed to harmonize chemical and biological control in peach orchards; insecticides and acaricides.

Simcoe, Ont.: J. A. Hall and one research officer; life-histories, habits, and control of apple insects; orchard spraying.

Harrow, Ont.: H. R. Boyce and two research officers; life-histories, habits, ecology, and control of stone-fruit and greenhouse insects.

Morden, Man.: H. P. Richardson; life-histories, habits, and control of fruit insects in the Prairie Provinces.

Summerland, B.C.: J. Marshall and six research officers; biology and control of tree-fruit insects; development of equipment for concentrate spraying; orchard spray formulations.

Creston, B.C.: W. H. A. Wilde; vectors of stone-fruit viruses.

Victoria, B.C.: H. Andison and three research officers; life-histories, habits, ecology, and control of insects affecting small fruits and ornamentals.

Investigations on fruit insects were under the direct supervision of the Dominion Entomologist until 1938, when the Fruit Insect Unit was established under Ross. He directed the work of the Unit until his retirement in 1955. Since then A. P. Arnason has been Acting Head.

Insecticide investigations of more general application were first conducted at the laboratory at Annapolis Royal and Kentville, N.S., under G. E. Sanders (1912-1921) and A. Kelsall (1921-1938). The Chemistry Division, Canada Department of Agriculture, participated in these studies in Nova Scotia from 1922 and has continued them since 1938; similar co-operative studies have been conducted at Summerland, B.C., since 1944. Ross was co-ordinator of the work on insecticides in the Division for many years. This led to the formation in 1949 of an information and reviewing service under W. S. McLeod until 1952 and L. A. Roadhouse since.

Co-operative studies have been undertaken with other entomologists, especially on biological control of the oriental fruit moth in Ontario and of the oystershell scale, the apple mealybug, and the woolly apple aphid in British Columbia, and recently on predacious mites and Hemiptera, also in British Columbia; with plant pathologists on virus diseases of stone fruits in Ontario and British Columbia, and on fungicidal sprays; with chemists on toxic residues and spray deposits; and with horticulturists and other agriculturists on entomological aspects of orchard practices. Much assistance has been given in various ways to provincial advisory services and grower organizations in promoting insect control. Grower organizations, especially the British Columbia Fruit Growers' Association and associations in Ontario, have given financial aid or other valuable help in furthering investigations on problems of vital interest to the industry.

Provincial departments in Ontario, British Columbia, and Nova Scotia were active in work on fruit insects during the early years of investigation in these provinces; those in Quebec and New Brunswick, somewhat later. After federal

laboratories were established the provinces gradually withdrew from this field, but have in all cases greatly increased the amount and effectiveness of advisory work. Entomologists at the agricultural colleges in Ontario, Nova Scotia, and Quebec have conducted studies on fruit insects but their main contribution has been in undergraduate and postgraduate training of students who were later employed by the federal government.

In Ontario, J. H. Panton of the Ontario Agricultural College conducted some investigations on fruit insects between 1891 and 1899 and his successor, Lochhead, had an active role early in the twentieth century in the development of control measures for the San Jose scale and other insects. Both men issued spray calendars for fruit insects. For at least five years, beginning in 1885, spraying demonstrations were held in about 30 orchards throughout the province. Similar demonstrations have been conducted by the Ontario Fruit Branch.

To meet the threat from the San Jose scale outbreak that began in 1897, the province passed its first regulatory legislation in 1898, supported extensive testing of control measures, and promoted a vigorous program of eradication and chemical control that brought the pest under control within a few years. In 1924 L. Caesar organized a spray service that directed the spraying operations of growers. This service and another in the Niagara district are still maintained in modified form. Since its formation in 1907 the agricultural representative service assisted in such extension work.

Caesar, who joined the staff of the Ontario Agricultural College in 1908 and was Provincial Entomologist from 1912 to 1940, devoted a large part of his effort to fruit insect work and provided notable leadership in orchard entomology. In research his most important contributions were on spray programs for the control of various pests; on the apple maggot, in co-operation with Ross; on fruit flies of cherry; and, in 1916, on evaluation of insecticidal dusts.

In British Columbia, concern over insects during the 1890's led to the passage by the province of the Horticultural Board Act of 1892, which provided for control of insect pests and employment of an inspector of fruit insects. Strict and energetic enforcement of import regulations, fumigation of nursery stock, and eradication of incipient outbreaks are claimed to have delayed the establishment of many fruit pests, including the codling moth and the San Jose scale. Members of the fruit inspection staff, notably T. Cunningham (1907 to 1916), the provincial horticulturists, especially R. M. Winslow (1909 to 1917), and the Provincial Entomologist G. W. Eastham and his assistant, M. H. Ruhmann, for many years after 1914, were responsible for the general adoption of control measures by fruit growers. Provincial officers conducted many investigations on fruit insects and their control well into the 1920's. From 1918 onwards the provincial research came under the direction of the federal entomologist in the Okanagan Valley. In recent years provincial activities consist chiefly of demonstration and other advisory work. Spray calendars prepared jointly by provincial and federal officers have been issued regularly. Through the years the British Columbia Fruit Growers' Association has given strong support for entomological activities of value to the fruit industry.

In Quebec, participation by the provincial department of agriculture in fruit insect work began after the first provincial entomologist, V. A. Huard, was appointed in 1913, and the Plant Protection Act was enacted by the province in 1914. The work, largely of a regulatory and extension nature, and of experimentation and demonstration of control measures, was under the direction of G. Maheux from 1916-1950 and has been under G. Gauthier since. Several entomologists are now engaged in the work. To encourage use of control measures,

assistance has been given growers to purchase spray equipment and a spray service organized in 1928 now serves most fruit growers in the province. The Pomological and Fruit Growers' Society of the Province of Quebec and the Quebec Society for the Protection of Plants have promoted fruit insect investigations and establishment of extension and other services in the province. Entomologists on the staff of Macdonald College and of the Institut agricole d'Oka, especially Lochhead and Father Leopold, have taken part in limited investigations of fruit insects at various times. The first spray calendar for Quebec was issued in 1909, another followed in 1921, and since 1928 calendars have been published annually.

Of the Maritime Provinces, only Nova Scotia has taken an extensive part in activities concerned with fruit insects. Except for inspection work for a few months in 1901 and 1902, and activities begun in 1907 on control of the newly discovered brown-tail moth, little was done until after the first legislation for regulation and control of insect pests was passed in 1911, and appointment of the first provincial entomologist in 1912. W. H. Brittain, while Provincial Entomologist (1913-1928), directed studies on many important pests, the more notable being on the apple maggot (1915-1917), the apple sucker (1919-1923), and the green apple bug, *Lygus communis novascotiensis* Knight. Under his supervision, an extensive study[139] from 1928 to 1932 on pollination of apple insects was completed. His successor, Pickett (1929-1939), made an exhaustive study of the apple maggot and allied species,[140] and on his advice a compulsory program of control of the apple maggot was instituted in 1931 to protect the overseas market for Nova Scotia apples. This action, under the supervision of the Apple Maggot Control Board, has been effective in freeing orchards of infestation. A comprehensive advisory service for the Annapolis Valley was begun in 1928 and soon served most of the fruit growers. In 1938 supervision by a provincial officer of all orchard practices was undertaken under contracts with associations of growers, and has been reasonably successful in improving the effectiveness of insect control practices. Spray calendars have been issued whenever necessary since 1916. Since the Second World War, the province has restricted its activities almost entirely to advisory and regulatory services.

Main Problems

About 300 species of insects and mites injurious to fruit in Canada have been recorded and studied. However, investigations have been mainly concerned with species of major importance, and much of the effort has been on chemical control and its integration into orchard practice. Emphasis has been on life-histories and ecology of various pest insects and mites and of their natural enemies; on insecticides, acaricides, methods of applying them, and their effects on the orchard fauna; on avoiding objectionable spray residues; on physiological and toxic effects of spray materials on fruit and foliage, accumulation and persistence of pesticides in soils, and their effects on soil fauna and flora; on entomological aspects of horticultural practices; and on insect and mite vectors of virus disease organisms of stone and small fruits. For insects of minor importance short studies on life-history and control have sufficed.

Spray Practices and Insecticides

Excellent reviews of the many developments in orchard spray practice have been given by Caesar,[141] Kelsall,[142] C. E. Petch,[143] Marshall,[144] and G. G. Dustan;[145]

139 Canada Dept. Agr. Bull. 162, n.s., 1933.
140 *Canadian J. Res.*, D, 53-75, 1937.
141 Ont. Dept. Agr. Bull. 462, 1948.
142 *Sci. Agr.* 19: 405-410, 1939.
143 50th Ann. Rept. Pomol. and Fruit Growing Soc. Quebec: 33-45, 1943.
144 Proc. Ent. Soc. B.C. 48: 25-31, 1952; 49: 7-11, 1953.
145 *Agr. Inst. Rev.* 8(2): 10-11, 14, 1953.

these cover developments from the earliest uses of insecticides on fruits almost to the present day. In the last three years a few new chemicals, notably ryania for control of the codling moth in the Maritime Provinces and Quebec and some acaricides, have come into use. After the Second World War, so many new insecticides and acaricides became available that testing in the orchard had to be on a highly selective basis. Consequently, a program for screening these chemicals in the laboratory was undertaken by T. Armstrong at Vineland Station, Ont. This has provided much useful information.[146] Promising materials were evaluated in orchard trials and information was obtained on compatibility with other chemicals, phytotoxicity, health hazards, persistence, residues, dosage and costs.[147]

San Jose Scale

Although the San Jose scale, *Aspidiotus perniciosus* Comst., was found as early as 1894 in British Columbia, it was not a serious pest of fruit in Canada until it was found in southwestern Ontario in 1897. Within a few years it destroyed more than two million trees in the best fruit districts and threatened to ruin the fruit industry of Ontario. Legislation prohibiting the importation of nursery stock or its movement from infested orchards was passed by the province of Ontario and the federal government in 1898. After 1900, movement was permitted after fumigation in stations established for that purpose. However, the destruction of infested orchards failed to eradicate it and, as no other effective control measures were known, the scale continued to spread. After much experimentation, the provincial scale inspector, G. E. Fisher, found a practical remedy, lime-sulphur, in 1902; soon afterwards the scale was no longer a problem. The new insecticide also proved to be a most valuable fungicide. The outbreak resulted also in the introduction of power spraying, and demonstrated the necessity of thorough spraying.

The scale has not been a problem elsewhere in Eastern Canada and even in southern Ontario it is now rarely troublesome, but in British Columbia economic infestations appeared between 1912 and 1915 and have been troublesome since. At present, dormant sprays of lime-sulphur and heavy petroleum oil are used effectively wherever threatening infestations appear. Summer sprays of parathion are also useful.

Apple Maggot

The apple maggot, *Rhagoletis pomonella* (Walsh), was first reported in Canada from apples in 1896. By 1913 serious infestations occurred in all provinces of Eastern Canada, but it is not yet a pest in British Columbia. Studies begun in 1911 by Caesar and by Ross[148] and in 1913 by Brittain and C. A. Good[149] elucidated the principles and practices, including the use of unsweetened arsenical sprays, required for control. This approach, with some modifications suggested by ecological studies by Hall[150] between 1933 and 1936 and by other observations, is still sound. When Great Britain threatened to place an embargo on Canadian apples infested with the apple maggot, Nova Scotia passed an Apple Maggot Control Act in 1931. Under this act a specified program of control had to be followed by growers producing for the export market. The enforcement, supervision, and inspection were placed under the Apple Maggot Control Board. Ontario, Quebec, and New Brunswick developed similar measures after 1932. In 1932, regulations under the Detructive Insect and Pest Act prohibited export

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146 Sci. Agr. 29: 81-85, 1949; Canada Dept. Agr., Sci. Serv. Res. Notes Ser., E-9, 1954.
147 84th Ann. Rept. Ent. Soc. Ont. (1953): 35-45, 1954.
148 Ont. Dept. Agr. Bull. 271, 1919.
149 N.S. Dept. Agr. Bull. 9, 1917.
150 67th Ann. Rtpt. Ent. Soc. Ont. (1936): 46-53, 1937.

of apples to the British Isles unless they were grown in orchards in which specified control measures were used and were certified to be free from infestation. Export of apples stored for six weeks at 32°-34°F. was also permitted because this killed any larvae in the apples. The Federal Apple Maggot Control Advisory Committee, established in 1934, has periodically reviewed accomplishments and has helped to formulate and co-ordinate policies and control requirements in the four provinces. The program prevented infested apples from entering the overseas market but has not eliminated the maggot, though infested properties in the control districts are fewer.

Codling Moth

For 50 years or more the codling moth, *Carpocapsa pomonella* (L.), has been potentially the most serious pest of apple and pear in Canada. Economic infestations were reported in Eastern Canada more than 100 years ago, but in British Columbia this pest did not become established until 1912, or widespread until 1925, because many incipient infestations were eradicated under the direction of the provincial authorities.[151] Once established in a district, the moth became a more and more serious problem. By the late 1930's and early 1940's control measures were no longer satisfactory in districts favourable for the moth and excess arsenical residues, until overcome a few years later, caused loss of the United States market for British Columbia apples. Growers were even advised not to plant apples in some districts. The pest is especially serious in southern Ontario and British Columbia, where two generations occur every year.

Before the advent of insecticides a measure of control was obtained by picking and destroying infested fruit and by trapping larvae by banding the tree trunks. Effective control with insecticides was first obtained about 1878 in Ontario with paris green. Lead arsenate came into use about 1910, and calcium arsenate, especially in the Maritime Provinces and Quebec, soon afterwards; emulsions of 1 per cent oil and lead arsenate in early sprays and nicotine in late summer sprays, in the early 1930's; cryolite or nicotine, including fixed nicotine, in the late 1930's; micronized phenothiazine in the 1940's; and DDT, about 1946. DDT was phenomenally effective. However, methoxychlor is also used now in British Columbia because of its lower mammalian toxicity and ryania is recommended in Nova Scotia and Quebec as it is less detrimental to natural enemies of orchard insects. In Ontario and British Columbia ryania has not proved wholly satisfactory. As the problem became more difficult, the number of applications increased from the one or two used early in the century to as many as eight in the 1940's, dropped to four after DDT became available, but is again increasing. Supplementary measures developed by A. A. Dennys and A. D. Heriot[152] in 1942, sprays against cocooned larvae and foliage sprays of sodium dinitrocresylate, did not come into use because of the advent of DDT. They may prove useful if present methods lose their effectiveness.

Studies on the life-history, habits, and ecology of the moth include those in the 1920's and 1930's by Hall[153] and by W. G. Garlick.[154] These indicated that some of the first-generation larvae went into obligatory diapause; that 25 per cent of the first-generation larvae entered at the side of the fruit in 1919 and 92 per cent in 1937; that larvae feed on leaves but few if any survive; and that many of the cocoons are formed in the crowns of the trees so that trunk sprays or traps are ineffective. Life-history and ecological data obtained by Beaulieu[155] resulted in better timing of sprays in Quebec, and nutritional studies by Heriot

151 Proc. Ent. Soc. B.C. 39: 16-19, 1942.
152 *Sci. Agr.* 22: 571-583, 1942.
153 59th Ann. Rept. Ent. Soc. Ont. (1928): 96-105, 1929.
154 69th Ann. Rept. Ent. Soc. Ont. (1938): 58-61, 1938; *Sci. Agr.* 28: 273-292, 1948.
155 *Sci. Agr.* 20: 624-631, 1940.

and D. B. Waddell[156] explained differences in susceptibility of adults and larvae to insecticides. Investigations in Nova Scotia[157] by Pickett and his associates are showing how the number of applications may be reduced to advantage in that region by using insecticides that are not detrimental to natural enemies.

Orchard Mites

The European red mite, *Metatetranychus ulmi* (Koch), the most important species, the two-spotted spider mite, *Tetranychus bimaculatus* Harvey, and the *Bryobia praetiosa* Koch complex are common everywhere in Canada. In British Columbia *Eotetranychus pacificus* (McG.), *E. carpini borealis* (Ewing), and *E. mcdanieli* (McG.) are also important. The pear leaf blister mite, *Eriophyes pyri* (Pgst.), was a serious problem early in the century, but has become unimportant where lime-sulphur or dormant oil sprays have been used. The European red mite, first found in Canada in Ontario in 1912 and soon thereafter in other provinces, has steadily increased in importance as a pest of fruit. This and other mite species became the most serious pests in orchards after DDT and parathion came into general use.

Intensive investigations on the life-history and control of the European red mite have been conducted in Ontario from 1913 to 1921 by Ross and W. Robinson;[158] in Nova Scotia from 1913 to 1934 by Gilliatt;[159] and in Quebec since 1950 by Beaulieu and B. Parent. Effective control was developed by Ross and his associates in the early 1920's with dormant sprays of three per cent lubricating oil emulsion or with summer lime-sulphur sprays; but these became progressively less satisfactory. In the late 1930's and the early 1940's, dinitro sprays came into use. Monoethanolamine dinitrocyclohexylphenolate, developed at the Summerland laboratory, in dilute sprays proved superior to others and appeared to have little effect on predators but was replaced by parathion and malathion in the late 1940's. However, strains resistant to these chemicals developed within three years in British Columbia and since then in Ontario. As a result of extensive greenhouse and orchard tests, several synthetic acaricides (Ovotran, Sulphenone, Aramite, and DNOCHP) have found a place in orchard sprays and even more satisfactory acaricides may be available in the near future.

The history of the two-spotted spider mite runs a parallel course, though it is perhaps a more serious pest of greenhouse crops and of small fruits than of tree fruits.

Investigations (to be published soon) by C. V. G. Morgan and N. H. Anderson during the last five years on the morphology, life-history, and habits of the *Bryobia praetiosa* complex confirmed E. P. Venables' suggestion in 1943 that this complex includes a tree-inhabiting form and another restricted to herbaceous vegetation.

The ecological studies by Pickett and his associates[160] in Nova Scotia, begun in 1943, have demonstrated that sulphur and iron carbamate sprays were harmful to the principal predators of the European red mite, and that when copper fungicides or glyodin was substituted predators increased rapidly so that the phytophagous mites again became unimportant. However, where DDT and parathion, which virtually eliminate all predators, are used the injurious species may quickly become troublesome, because their short life-cycles permit rapid increases from small populations surviving treatment. These studies are providing much information on the various species of mites and insects that prey on

156 *Sci. Agr.* 23: 172-175, 1942.
157 *Canadian Ent.* 85: 472-478, 1953.
158 42nd Ann. Rept. Ent. Soc. Ont. (1921): 33-42, 1922.
159 *Canadian J. Res.*, D, 13: 1-17, 1935.
160 *Canadian Ent.* 81: 202-214, 217-230, 1949; 88: 129-137, 1956.

phytophagous mites as well as on how control programs may be modified to reduce the abundance of pest species through the action of beneficial forms. Similar studies on the mite problems in peach orchards are under way by W. L. Putman and by Boyce in Ontario; in apple orchards by E. J. LeRoux, O. Paradis, and Parent in Quebec, and by Morgan and his associates in British Columbia; and on small fruits by Richardson in Manitoba.

Oriental Fruit Moth

The oriental fruit moth, *Grapholitha molesta* (Busck), found in the Niagara district of Ontario in 1925, spread rapidly throughout peach orchards of the province and, as no effective control measures were available. it caused great concern to growers. Beginning in 1926, Ross, Putman, Dustan, W. E. van Steenburgh, C. W. Smith, and Boyce reported on effects of cultural practices, parasites, predators, weather, and host relations on abundance and damage. Chemicals available in the 1930's gave unsatisfactory control. However, the parasite *Macrocentrus ancylivorus* Roh., introduced in 1929, and native parasites and predators brought infestations and damage down to relatively low levels for several years in the 1930's.[161] After 1943, losses were again serious. Between 1946 and 1950 Dustan, Putman, and Boyce[162] developed a spray program using DDT, parathion, or EPN. With the help of parasitism by *M. ancylivorus*, which is not affected by the spray program, this provides satisfactory control.[163] This insect has not been found elsewhere in Canada.

Leaf Rollers, Bud Moths and Fruitworms

The eye-spotted bud moth, the gray-banded leaf roller, the oblique-banded leaf roller, the strawberry leaf roller, the red-banded leaf roller, and the green fruitworm have been serious pests of fruits in Eastern Canada since the early days of orchard entomology. In British Columbia the eye-spotted bud moth and the boxelder leaf roller have been important fruit pests. Extensive investigations were made on this group of insects in Nova Scotia in the 1910's by Sanders and A. G. Dustan[164] and between 1922 and 1938 by F. C. Gilliatt, whose papers included a detailed study of the bionomics of the gray-banded leaf roller;[165] and in Ontario by Hall[166] on identification, biology, and control. In recent years the red-banded leaf roller and the eye-spotted bud moth have been troublesome where DDT has been used.

Insects of Ornamentals and Greenhouse Crops

Investigations on insect pests of ornamental plants and greenhouse crops have been conducted by the Fruit Insect Unit. These have largely been short-term, practical tests of control measures for various pests at the laboratories at Vineland Station and Harrow, Ont., and Victoria, B.C. In 1940 the available information on greenhouse insects was published by A. Gibson and Ross[167] and in 1953 Boyce[168] gave the latest recommendations. Gibson[169] published a similar compilation in 1934 for insects of the flower garden. The synthetic insecticides and acaricides and the aerosols and smokes introduced since 1945 have simplified and improved the control of most of these pests.

The narcissus bulb fly, *Lampetia equestris* (F.), was a serious pest in commercial bulb nurseries in British Columbia until Andison[170] developed a simple treatment of the soil and bulbs at planting time with aldrin, dieldrin, heptachlor,

161 69th Ann. Rept. Ent. Soc. Ont. (1937): 65-74, 1938.
162 81st Ann. Rept. Ent. Soc. Ont. (1950): 50-72, 1951.
163 85th Ann. Rept. Ent. Soc. Ont. (1953): 48-55, 1954.
164 Canada Dept. Agr., Ent. Branch Bulls. 16 & 17, 1919.
165 Trans. Roy. Soc. Canada, 3rd Ser., 23 (Sec. V): 69-84, 1929.
166 64th Ann. Rept. Ent. Soc. Ont. (1933): 21-31, 1934.
167 Canada Dept. Agr. Pub. 695, 1940.
168 *Agr. Inst. Rev.* 8(2): 36-38, 1953.
169 Canada Dept. Agr. Bull. 99, n.s., 1928.
170 Canada Dept. Agr. Pub. 905, 1954.

or chlordane. This provides excellent protection for at least three years. In 1949 and 1950 Andison and W. T. Cram devised a method of fumigating the bulbs with methyl bromide immediately after they are dug. This provides the first effective means of eliminating infestations in bulbs in storage, previously the cause of severe losses.

Biological Control

Introduced parasites and predators have provided outstanding control of fruit insect pests in a few instances. The role of parasites against the oriental fruit moth has been indicated. Three other instances, all in British Columbia, are noteworthy. The mite *Hemisarcoptes malus* (Shimer), introduced into British Columbia from Nova Scotia by J. D. Tothill and Treherne in 1917, has been a major factor in keeping the oystershell scale in check. The parasite *Aphelinus mali* (Hald.), introduced in 1929, virtually eliminated the woolly apple aphid-perennial canker problem. *Allotropa utilis* Mues. was almost equally effective, though slower, in controlling the apple mealybug.

Limited success in use of disease organisms was achieved by A. G. Dustan[171] with the fungus *Entomophthora sphaerosperma* Fres. against the apple sucker, *Psylla mali* (Schmdb.), in Nova Scotia.

Harmonizing Chemical and Biological Control

Interrelations of the apple orchard fauna and effects of spray materials on them have been studied in Nova Scotia by Pickett and his associates since 1943. Complementary studies are under way in Quebec and British Columbia and similar studies were begun in 1947 by Putman in peach orchards in Ontario. These investigations were undertaken because insect species that were unimportant early in the century had become troublesome even though more effective insecticides and improved methods of application were in use. Two papers by Pickett[172] outlining the principles on which the study is based have attracted attention. The results[173] are already influencing pest control policies. They have shown that the change to pest status of some species was the result of destruction by chemicals of the predators and parasites that formerly kept them in check and that when the chemicals least detrimental to beneficial species were used many pest species were held at non-injurious levels. By modifying the chemical control program both in regard to materials and to timing of applications, the cost of control in Nova Scotia has been reduced by as much as half the cost of materials. Similar results are being obtained in Quebec, but they have been less encouraging in the warmer districts of Ontario and British Columbia[174] because of the greater complexity of the problems there. Studies are continuing in Nova Scotia and elsewhere in Canada on the practical possibilities of using artificial control methods that supplement, rather than replace, natural controls.

Concentrate Sprayers

During the past ten years, a team of entomologists, chemists, horticulturists, and an engineer led by Marshall pioneered research on the development of concentrate sprayers[175] for orchard spraying that has received world-wide attention. The first successful sprayer, a light, automatic machine operated by the tractor driver alone and using an air blast to carry the insecticide to the trees, was designed in 1948. Commercial concentrate sprayers based on this design are now used in more than 90 per cent of the orchards in British Columbia. Spray

171 *J. Econ. Ent.* 20: 68-75, 1927; Canada Dept. Agr. Pam. 45, n.s., 1934.
172 79th Ann. Rept. Ent. Soc. Ont. (1948): 37-41, 1949; *Canadian Ent.* 81: 57-76, 1949.
173 *Canadian Ent.* 85: 472-478, 1953.
174 *Canadian Ent.* 88: 1-5, 1956.
175 *Agr. Inst. Rev.* 8(2): 67-69, 1953.

formulations have also been modified to obtain a uniform, effective dosage in all parts of the tree with as little as 50 to 100 gallons of spray per acre. Concentrate sprays are satisfactory against the principal orchard pests at savings of up to 75 per cent in labour and 25 per cent in materials and have eliminated much of the unpleasantness associated with conventional spray practice. The sprayer is being tested and is coming into use in other parts of Canada where orchard practice, weather, and insect development are different. Adaptations of the sprayer are being introduced in Australia, the United States, and elsewhere.

Other Problems

Outstanding contributions to knowledge about biology and control of other fruit insects include: determination of life-histories and host plants of several species of aphids by Ross between 1912 and 1918; the first effective control of the pear psylla by Ross and his associates during the early 1920's by means of a dormant spray of three per cent lubricating oil emulsion; control of the apple curculio with cryolite in the late 1930's, and of the round-headed apple tree borer with raw linseed oil-calcium cyanide mixture in 1928, by Petch,[176] the mixture being effective against other borers elsewhere; cultural and chemical control of the pear thrips by A. E. Cameron and Treherne, the treatment changing the status of the pest from that of the most serious on pear on Vancouver Island to a non-economic level; the first practical chemical control of the strawberry root weevil with raisin-shorts-sodium fluosilicate bait, developed by W. Downes, and an even more practical and effective control with a soil application of aldrin, dieldrin, chlordane, or heptachlor, developed by Andison and Cram since 1950, the last treatment also controlling white grubs, *Polyphylla perversa* Csy.; demonstration that the high humidity in fields sprinkler-irrigated or mulched with sawdust resulted in increased survival of the black vine weevil in strawberry fields; discovery by Maxwell that the strawberry weevil overwinters in the strawberry plantation and not in surrounding fields; discovery by G. W. Wood that the feeding of *Franklinella vaccinii* Morgan on first-year growth of blueberry may cause failure of the crop the following year; development by Richardson of practical controls of insect pests of small fruits on the prairies; control of the plum curculio in Quebec and Ontario with dieldrin sprays; and evidence that the present spray programs in British Columbia will not result in dangerous contamination of the soil.

Stored Product Insects

Emphasis in stored product insect work has been on the safe storage and transport of grain and grain products for domestic and export trade. Most of the applied research is conducted by the Entomology Division through its laboratories at Ottawa, Winnipeg, and Vancouver; and advisory services to the Board of Grain Commissioners, Department of Trade and Commerce, are likewise provided from these centres. Fundamental studies of the physiology of certain stored product insects are in course at the Ottawa laboratory and at several universities and colleges in Ontario and Quebec. In all, less than a dozen Canadian entomologists are working in this field.

In stored grain, the most serious pests are the Indian-meal moth, *Plodia interpunctella* (Hbn.), the rusty grain beetle, *Laemophloeus ferrugineus* Steph., and the grain mite, *Acarus siro* L. Spider beetles, of which there are a dozen species, are the most important in flour storage warehouses; other injurious species include the white-shouldered house moth, *Endrosis sarcitrella* (L.), and the brown house moth, *Hoffmannophila pseudospretella* (Staint.). In flour mills and food-manufacturing plants, the most troublesome forms are the confused

176 *Sci. Agr.* 8: 560-566, 1928.

flour beetle, *Tribolium confusum* Duv., the flat grain beetle, *Laemophloeus pusillus* (Schönh.), and the Mediterranean flour moth, *Anagasta kühniella* (Zell.). The low temperatures of Canadian winters retard the activities of many of these pests and benefits accrue from loading and shipping in cold weather. Nevertheless, reliance in control is upon the proper use of fumigants.

Although the Stored Product Insect Unit in the federal department was not established until 1948, insects infesting stored grain and other products have been problems since the very beginning of entomological work in Canada. In the early days, such problems were handled by officers studying pests of the field and orchard, but since 1932 one or more federal entomologists have worked continuously on stored product insects.

About the end of the nineteenth century, several insects in this group became important in Canada. The pea weevil, *Bruchus pisorum* (L.), was found by James Fletcher in 1884 to be abundant in Canadian seed collections and by 1902 was causing an estimated loss of at least one million dollars annually. This damage resulted in a drastic reduction in the acreage of this crop in Canada. In 1889 Fletcher discovered the Mediterranean flour moth in Ontario. This was also the first record for North America; and in a country-wide survey of flour mill insects by Arthur Gibson in 1916 it was the most important pest encountered. In 1898 the bean weevil, *Ancanthoscelides obtectus* (Say), was recorded for the first time as a pest in Canada. It is now widely spread and common in stored beans.

In 1913 W. A. Ross carried out the superheating of a flour mill and feed storage in Dundas, Ont., to control the Mediterranean flour moth. This was the first use in Canada of high temperature to control insects in a processing plant.

C. G. Hewitt, the second Dominion Entomologist, was very interested in this field of entomology. In 1916 he served with C. J. S. Bethune, Ontario Agricultural College, and E. M. Walker, University of Toronto, on a committee of the Royal Society of Canada to investigate the economic importance of insects infesting stored grain and to suggest control measures.[177]

In 1919 E. H. Strickland, then a federal government employee, studied the economic species of mites infesting stored grain in eastern terminal elevators, and the insect pests of flour mills and of dried fruits. Arthur Gibson observed the life-histories and habits of a number of stored product pests. From 1924 to 1928 he was assisted in this work by C. H. Curran, who published a list of the common pest species as well as a paper on the identification of adult lepidopterous insects attacking stored products. In 1929 Gibson and C. R. Twinn published a bulletin, *Household Insects and Their Control*, in which most of the common stored product pests were discussed and illustrated. Revised editions appeared in 1931 and 1939.[178]

In 1931 an extensive examination was made of Canadian grain in elevators throughout Canada. The following year Twinn carried out an investigation of grain in the terminal storages at Fort William and Port Arthur, Ont. Infestations of mites were found in the bottoms of some bins. As a result of these findings it has become common practice to clean the last thousand bushels of grain from the bottom of a bin before loading out, and to sweep thoroughly and clean bins before re-use.

Serious infestations in Western Canada of the hairy spider beetle, *Ptinus villiger* (Reit.), led to the appointment of H. E. Gray in 1932 as officer-in-charge of stored product insect investigations, directly under the Dominion Entomologist.

177 Proc. Roy. Soc. Canada, 3rd Ser., 11: XIII-XVI, 1917.
178 Canada Dept. Agr. Pub. 642, 1939.

A temporary laboratory was established in Winnipeg, where the spider beetle problem was studied in co-operation with the Canadian National Millers' Association and member mills, and control measures were devised. Similar problems have since occurred with *Ptinus ocellus* Brown on the west coast and with *Ptinus raptor* Sturm in the Maritimes.

In 1934, Gray conducted a survey of flour mills in Eastern Canada, and, in co-operation with the Canadian trade commissioners to Norway, undertook a systematic examination of the flour shipments being sent to Norway and of the ships carrying such cargoes. The carriers were found to be completely free from insect pests, but most of the mills were infested. These surveys did much to smooth relations between the millers and the Norwegian Corn monopoly. Through regular checking, and meetings at which sanitation was discussed, much was done to improve the conditions in mills throughout Canada. This policy was continued throughout the period of the Second World War.

In 1934 Gray began a series of inspections of lake carriers both in connection with claims and to determine the fitness of laid-up lake tonnage for winter storage cargoes. A standard inspection technique was developed and with the outbreak of war in 1939 a program of lake and ocean-going ship inspection was initiated. The inspectors of the Plant Protection Division were trained in these phases of the work. This program proved so beneficial that it has become standard procedure at all Canadian ports.

With the ouberak of the Second World War and the necessity for long-time storage of grain, stored product insect problems multiplied. In 1940 a serious outbreak of the Indian-meal moth occurred in several Georgian Bay elevators. Use of annexes and other temporary storage brought problems with the grain mite and the rusty grain beetle. B. N. Smallman, appointed as a grain inspector to the Board of Grain Commissioners in 1941, was seconded to the Entomology Division to study grain problems in premises under the jurisdiction of the Board. H. H. J. Nesbitt, now of the Department of Biology, Carleton College, Ottawa, served on the Ottawa staff from 1936 to 1948. During the war he studied the biologies and taxonomy of mites affecting grain in storage. One of the major war-time accomplishments was the maintenance of grain storage facilities in essentially insect-free condition, ensuring a continuous supply of clean food for overseas requirements.

After the war, Smallman and B. Berck, a chemist of the Grain Research Laboratory at Winnipeg, were transferred from the Board of Grain Commissioners to the Entomology Division, and the Winnipeg laboratory was re-established in 1946 with Smallman in charge. As a result of tests of the newer insecticides, better control of flour mill insects was provided, and losses from spider beetles in flour warehouses were almost eliminated through regular use of DDT sprays. Smallman and S. R. Loschiavo[179] began a study of the food preferences of certain flour mill insects. In 1951, when Smallman was transferred to the Science Service Laboratory, London, Ont., F. L. Watters was appointed Officer-in-Charge at Winnipeg. Experiments were then centred on spot fumigants,[180] contact and residual sprays of the newer insecticides, and sterilizing procedures to assist the miller. At present studies are under way on the distribution, concentration, and effectiveness of fumigants in bulk grain.

The Vancouver laboratory was established in October, 1949, with J. H. Follwell in charge. He was succeeded in 1952 by P. Zuk. The biology and control of the Australian spider beetle, *Ptinus ocellus* Brown, is the main project of this laboratory.

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179 *Cer. Chem.* 29: 91-107, 1952.
180 *Cer. Chem.* 40: 343-348, 1953.

Insects Affecting Man and Animals

Developments in Canada relating to insects affecting man and animals are presented in this section under three general headings: biting flies, livestock insects, and household insects.

A large part of the work on these pests has been done by entomologists of the Canada Department of Agriculture, but a number of universities and provincial departments have also contributed. In the federal department the Veterinary and Medical Entomology Unit is primarily responsible. This unit was formed in 1952 by amalgamation of the units Livestock Insect Investigations and Household and Medical Entomology, both of which were established in 1948 from entomologists and laboratories hitherto operating directly under the Chief of the Entomology Division. This field of work first received serious attention about 1912. It grew slowly until after the Second World War, but by 1956 between 35 and 40 entomologists at some 17 locations are engaged in it, about two-thirds of them in the federal service at laboratories in Ottawa, Guelph, Saskatoon, Lethbridge, and Kamloops.

Biting Flies

Although certain species of mosquitoes have been implicated in the transmission of encephalomyelitis, and certain species of black flies are carriers of blood parasites of ducks, turkeys, and other birds, the problem of biting flies in Canada is mainly one of severity of attack rather than of disease transmission. In areas where they are abundant they often make life difficult for man and beast and seriously hinder outdoor activities.

Before 1920 little was known about these insects. E. Hearle was the first to make a careful study of mosquitoes in Western Canada. He investigated the mosquitoes of the Lower Fraser Valley, B.C., in 1919-1921[181] and between then and 1934 added much to the knowledge of mosquitoes in the Rocky Mountain region of Alberta and on the prairies, particularly in Saskatchewan. After an epidemic of encephalomyelitis in 1941, J. G. Rempel, University of Saskatchewan, studied possible vectors in Saskatchewan, and published important papers on the mosquitoes of Western Canada.[182] C. R. Twinn commenced a study of mosquitoes in Eastern Canada in 1924 and, in subsequent years, presented the results in a number of papers, including a review of the more important mosquito problems in Canada and a summary of the species distribution.[183] In 1937-1938 C. G. MacNay[184] made field tests of mosquito repellents.

A survey of anopheline mosquitoes in the vicinities of military hospitals across Canada was undertaken in 1944 in co-operation with the medical services of the armed forces by entomologists and associated workers in the Entomology and Plant Protection divisions and in provincial services. A report on the survey was published by Twinn.[185]

Early work on Canadian black flies included an investigation of a cattle-infesting species in Saskatchewan by A. E. Cameron,[186] observations on the black flies of British Columbia by E. Hearle,[187] and a study of the black flies of Eastern Canada by Twinn.[188] More recently D. M. Davies,[189] McMaster University, made a quantitative study of black flies in a stream in Algonquin Park, Ont.

181 Natl. Res. Council Rept. 17, 1926.
182 *Canadian J. Res.*, D, 28: 207-248, 1950; *Canadian J. Zool* 31: 433-509, 1953.
183 *Mosquito News* 9: 35-41, 1949.
184 *Canadian Ent.* 71: 38-44, 1939.
185 Proc. 32nd Ann. Meet. New Jersey Mosq. Exterm. Assoc.: 242-251, 1945.
186 Canada Dept. Agr. Tech. Bull. 5, n.s., 1922.
187 Proc. Ent. Soc. B.C. 29: 5-19, 1932.
188 *Canadian J. Res.*, D, 14: 97-150, 1936.
189 Trans. Roy. Canadian Inst. 28: 121-160, 1950.

The first important contribution on horse flies and deer flies was a paper on the bionomics of the Tabanidae of the Canadian prairies by Cameron.[190]

During the Second World War various repellent materials from British, Canadian, and United States sources were tested against mosquitoes and black flies under field conditions by officers of the Entomology and Plant Protection divisions under the direction of Twinn. The results of these tests, carried out in areas in both Eastern and Western Canada, were made available to the military authorities of the three countries but were not published.

Since 1947, at the request of the Defence Research Board, Department of National Defence, the Entomology Division and co-operating agencies have given special attention to the study of biting flies, particularly in northern areas. The work is reviewed periodically by an advisory group known as the Entomological Research Panel appointed by the Board.

Field stations for studying the insects were maintained at Churchill, Man. (1947-1953), Whitehorse, Y.T. (1949-1953), and Goose Bay, Labrador (1949-1953). The Defence Research Board, the R.C.A.F., and the Canadian Army gave assistance and co-operation, especially in experiments in the control of biting flies with insecticides applied by airplane and ground equipment, and in facilities for biological as well as control studies. Several university professors also assisted, and a number of United States entomologists took part in the program from time to time. The United Kingdom sent observers in 1950 and 1951. Some of the work is also carried out at Entomology Division laboratories at Ottawa, Ont., Saskatoon, Sask., Lethbridge, Alta., and Kamloops, B.C., the western laboratories being particularly concerned with biting-fly problems affecting agriculture. In 1954, with assistance from the Pulp and Paper Research Institute of Canada, the work was extended to include biting-fly problems of the pulp and paper industry, the studies being made from temporary field stations in pulpwood cutting areas in Quebec.

As a result of this and earlier work, nearly 300 species of blood-sucking flies have been recorded in Canada, including 63 species of mosquitoes (Culicidae), about 72 of black flies (Simuliidae), at least 130 of horse flies and deer flies (Tabanidae), and 30 or more of biting midges (Ceratopogonidae). As these species all have different life-histories and habits, they present a complex and difficult problem. Many of the species are restricted to southern Canada, the number of species progressively diminishing northward. Some of the northern species, favoured by their environment, occur in enormous numbers. The problem is worst in the northern zone of transition between forest and tundra, such as at Churchill, Man. Beyond the tree line on the arctic tundra mosquitoes are the major pest but, fortunately, tabanids do not occur, and black flies are much less troublesome than in the forest.

Much has been learned about the life-histories and habits of many of the species. Chemical control measures have been developed that are reasonably effective against mosquitoes and black flies south of the tree line, when properly applied. Chemical control is still of doubtful value against tabanids because of the nature of their breeding places and habits, and not enough is yet known about the life-histories of the biting midges to allow effective action against their immature stages. The value of suitable clothing, shelter, and use of repellents in providing personal protection where area control is not practicable has been demonstrated.

Since 1947 more than 100 papers by about 50 authors have been published in scientific journals reporting the results of the investigations. Under the various

190 Bull. Ent. Res. 17: 1-42, 1926.

headings the following made valuable contributions. *Mosquitoes*: behaviour, A. W. A. Brown, J. A. Downes, W. O. Haufe; development, W. O. Haufe; rearing, W. E. Beckel, J. McLintock; and systematics, W. E. Beckel, J. R. Vockeroth. *Black flies*: life-histories, habits, and control, F. J. H. Fredeen, B. Hocking, D. G. Peterson; seasonal emergence, F. P. Ide; behaviour, D. M. Davies; and systematics, F. J. H. Fredeen, G. E. Shewell. *Tabanids*: bionomics, L. A. Miller. *Biting midges*: systematics, life-histories, and habits, J. A. Downes. *Biting flies (general)*: distribution, T. N. Freeman; dispersal, B. Hocking, D. W. Jenkins, J. A. Shemanchuk; use of precipitin test in identifying blood meals, A. E. R. Downe, G. S. Eligh, A. S. West; natural control, H. G. James; repellents and personal protection, A. A. Kingscote, D. G. Peterson, L. A. O. Roadhouse; and chemical control, A. W. A. Brown, L. C. Curtis, H. Hurtig, W. C. McDuffie, D. G. Peterson, J. F. Sharp, C. R. Twinn.

Reviews of the work have been presented by Twinn,[191] who directed or co-ordinated many of these studies. Revised departmental publications on the control of mosquitoes and black flies[192] were issued recently, and the draft was completed of an interservice manual on pest control that deals with biting flies as well as other insect and rodent problems of concern to the armed forces in Canada.

Livestock Insects

Biting flies, which affect livestock as well as man, are dealt with in the preceding paragraphs.

The first important studies of insects affecting livestock were commenced at Agassiz, B.C., in 1912, by S. Hadwen, an officer of the Health of Animals Branch of the Canada Department of Agriculture, and continued by Hadwen and A. E. Cameron at Saskatoon, Sask., in 1917. Hadwen published new knowledge on cattle warbles[193] and, with Cameron, on horse bots.[194] Papers were also published on biting flies on the prairies. In 1923 Hadwen prepared the first departmental bulletin on insects affecting livestock.

E. Hearle made surveys and investigations of livestock insects throughout southern sections of the Prairie Provinces, from Indian Head, Sask., 1926-1927, and in British Columbia, from Kamloops, 1928-1934. With the co-operation of local ranchers he established a large-scale warble control project at Tranquille, B.C., in 1931. He wrote several papers on blood-sucking flies and ticks and prepared the manuscript of the comprehensive departmental bulletin *Insects and Allied Parasites of Livestock and Poultry in Canada*,[195] which was published posthumously.

In 1937 a permanent laboratory was built at Kamloops for study of insects affecting man and animals. G. A. Mail was in charge and was succeeded by J. D. Gregson in 1943. From 1938 to 1953 the building was shared by Dr. F. H. Humphreys and a small staff from the Department of National Health and Welfare who were engaged in studies of plague, spotted fever, and other arthropod-borne diseases in Western Canada. In 1938-1940, entomologists at Kamloops assisted in surveys of rodents and their ectoparasites in British Columbia and Alberta. Studies begun in 1938 gave rise to a number of publications and culminated in two monographic works: *The Siphonaptera of Canada*,[196] by G. P. Holland, and *The Ixodoidea of Canada*,[197] by Gregson. At Kamloops particular

191 *Caandian Ent.* 84: 22-28, 1952; *Arctic* 7: 279-283, 1954; *Mosquito News* 15: 195-203, 1955.
192 Canada Dept. Agr. Pubs. 936 and 840, 1955.
193 Canada Dept. Agr., Sci. Ser. No. 27, 1919.
194 Bull. Ent. Res. 9: 91-106, 1918.
195 Canada Dept. Agr. Pub. 604, 1938.
196 Canada Dept. Agr. Pub. 817, 1949.
197 Canada Dept. Agr. Pub. 930, 1956.

attention is now being given to population dynamics of cattle warbles by G. B. Rich and to tick paralysis by Gregson. Tick paralysis, produced in British Columbia by *Dermacentor andersoni* Stiles, was first recorded in the Province in 1913 by Hadwen. It affects principally sheep, dogs, and man, and occasionally cattle and wildlife. The paralysis is believed to be caused by a neurotoxin secreted by the salivary glands of the female tick. Several papers reporting results of studies on the problem have been published by Gregson, F. J. O'Rourke, I. Rose, the Irving Clinic, Kamloops, and M. F. Murnaghan, University of Ottawa, but it still remains an enigma.

In 1947 a livestock insect laboratory was established at Lethbridge, Alta. R. H. Painter, who had directed a warble-fly control campaign in the Prairie Provinces since 1942, was in charge until 1953, when he was appointed Livestock Insect Liaison Officer for Western Canada and was succeeded by W. O. Haufe. Special attention is given at this laboratory to cattle warbles, lice, the sheep ked, and the horn fly.

In Western Canada rotenone sprays have proved inadequate in controlling warbles in free-ranging herds, especially when only one application a season is practical. Accordingly, emphasis is being placed on ecological and physiological studies of the insects. J. Weintraub has recently developed a technique for inducing reared warble flies to mate and lay eggs in captivity that will facilitate these studies and greatly enhance the prospects of developing more effective control measures.

W. A. Nelson has shown that the sheep ked has no significant effect on gains in weight of properly fed lambs; also that rams are much more heavily infested than wethers or ewes, and for a longer period, emphasizing the need of treating rams with insecticide before placing them with ewes in ked-free flocks. The life-history and habits of the horn fly were reviewed by J. McLintock and K. R. Depner,[198] including observations in southern Alberta.

W. O. Haufe has demonstrated that malathion and dieldrin are more effective against cattle lice than DDT, toxaphene, lindane, or rotenone. At least one gallon of emulsion spray per cow is required to wet mature range animals thoroughly enough for effective control. Other developments in control at this laboratory include a satisfactory method of spraying sheep to replace dipping, and a procedure for spraying ranch cattle and large herds.

In 1954 a livestock insect laboratory, with D. G. Peterson in charge, was established at Guelph, Ont., to serve Eastern Canada. Studies have been started on the physiology, natural mortality, and development of cattle warbles, the latter to enable better timing of control applications. Earlier studies[199] in this area by the Ontario Department of Agriculture showed that two or three applications of rotenone sprays or washes to the backs of cattle each season for several seasons caused a substantial, progressive reduction in warble infestation, and also that rotenone is highly toxic to swine. Poultry ectoparasites are also being investigated at this laboratory. Tests in southwestern Ontario showed that malathion is superior to other chemicals now used in controlling lice and mites on poultry.

Household Insects

Various species of household insects often cause annoyance and discomfort and sometimes damage to property in human habitations in Canada. Papers relating to various species of these insects have been published by a number of authors, notably C. G. Hewitt, A. Gibson, C. R. Twinn, C. G. MacNay, and G. J. Spencer.

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198 *Canadian Ent.* 86: 20-33, 1954.
199 81st Ann. Rept. Ent. Soc. Ont. (1949): 76-80, 1950.

In 1929 Gibson and Twinn brought together available information in the departmental bulletin *Household Insects and Their Control.* This was revised in 1931 and 1939[200] and had a wide distribution. It was later supplemented by a series of smaller departmental publications. The pest control industry, which was becoming established in many Canadian cities and towns during this period, was aided materially by this publication. The Canadian Pest Control Operators Association, which represents this industry, held its organization meeting in Ottawa in 1952.

In 1940-1941 Twinn and MacNay[201] tested various insecticides against head lice on school children at Ottawa with the co-operation of the local health department, and against crab lice and itch mites on military personnel at Petawawa and Camp Borden, Ont., with the co-operation of the Royal Canadian Army Medical Corps.

The resistance of the house fly to DDT was studied at Ottawa, 1949-1952, by L. A. O. Roadhouse.[202] He found that whereas in 1949 the average resistance of flies collected at various points in Ontario and Quebec was 20 times that of susceptible laboratory flies, by 1951 it had increased to 2000 times. By 1952 resistance was found in flies from localities in every province from Quebec to British Columbia.

Apiculture

The earliest experiment on honey bees in Canada was conducted in 1749.[203] Commercial beekeeping was apparently well established in the Province of Quebec by 1870, when some 46,000 colonies reportedly produced 648,000 pounds of honey.

Since the beginning of the twentieth century the beekeeping industry in Canada has experienced two periods of rapid expansion. These occurred during the two world wars, when sugar supplies were drastically reduced. Shortly after the First World War, honey stocks accumulated temporarily and an export market was begun. When sugar supplies returned to normal after the Second World War, the export market was not resumed because of dollar shortages in the United Kingdom and other European countries. Stocks of honey accumulated again and prices dropped rapidly to values approaching the costs of production.

Since 1947 the industry has undergone a period of retrenchment, the number of colonies being reduced by 46 per cent and that of beekeepers by 64 per cent. The 1955 statistics, however, indicate a levelling off, 323,600 colonies being operated by 14,150 beekeepers. A gradual rise in honey prices within the past few years and increased use of honey bees for pollination of fruits, vegetables, and legume crops have stimulated a broader interest in the industry. Since 1950, the average annual production of honey has been 28.8 million pounds and it has been necessary to import honey to meet the demand.

Improvements in effieciency of beekeeping have resulted from several factors: research; teaching and extension; organization on district, provincial, and national levels; and legislation for the control of diseases, honey grading, and purity of food.

Research

The Canada Department of Agriculture began its interest in the beekeeping industry in 1889 with the establishment of an experimental apiary at Brandon, Man. Some four years later another experimental apiary was established at the Central

200 Canada Dept. Agr. Pub. 642, 1939.
201 *Canadian Ent.* 75: 1-13, 1943.
202 *Canadian Ent.* 85: 304-346, 1953.
203 *Beekeeper* 35: 45, 1927.

Experimental Farm, Ottawa. The program of work was expanded in 1913 on the appointment of a full-time apiculturist. Apiaries were organized at experimental farms in all provinces. The early research dealt with problems in apiary management, such as swarm control, wintering, queen rearing, supering, and methods of preparing new colonies.

With the expansion in production that occurred immediately after the First World War, a considerable quantity of honey that was carried over in storage fermented. Studies on the biological and chemical constituents of honey were undertaken by the divisions of Chemistry, Bacteriology, and Apiculture. These studies provided basic information on the osmophilic yeasts that cause fermentation. The chemical analyses provided the basis for establishment of grades for honey with respect to moisture content. From 1929 to 1931 E. J. Dyce,[204] Ontario Agricultural College, developed a process whereby honey is heated to prevent fermentation and to promote recrystallization. This treatment, known as the Dyce process, is in current use by 18 packing-house establishments in Canada as well as several in the United States.

The increased volume of honey entering commercial packing plants necessitated the development of new equipment for processing honey. A commercial unit of the plate-type design was modified, and a tubular heat exchanger developed to pasteurize and cool honey on a continuous-flow basis. G. F. Townsend, Ontario Agricultural College, designed another tubular heat exchanger and developed a pressure sand-strainer that may be used to clarify honey as it is extracted, and by changing to a finer sand may also be used during the processing operation.

Studies on the chemotherapeutic control of brood and adult diseases of the honey bee have reduced losses to beekeepers substantially. C. A. Jamieson, in co-operation with H. Katznelson, Bacteriology Division, demonstrated that terramycin[205] and achromycin inhibit development of American foulbrood. In 1951 they[206] showed that the antibiotic fumagillin controls nosema disease in adult bees. This preparation is in current use by beekeepers in many parts of the world.

One of the obstacles in the development of a superior stock of bees has been the lack of information on the mating flight range of the queen. Recent studies by D. F. Peer,[207] Apiculture Division, Ottawa, on the mating flight behaviour of the queens have shown that breeding apiaries need to be ten miles apart in order to control matings.

Pollination studies[208] in Nova Scotia (1928-1932) by the Experimental Farms Service showed that honey bees were effective pollinators of apple trees. In recent years investigations by E. A. Karmo, Truro Agricultural College, N.S., have shown that maximum pollination can be obtained with the use of imported pollen placed at the entrances of colonies. This is particularly useful where varieties are grown in solid blocks. Similar studies on pears have been done at the Ontario Agricultural College. With the use of fluorescent marking compounds it has been possible to trace the foraging activity of bees on fruit bloom and on other crops. The pollination requirements of red and alsike clovers have been investigated by the Experimental Farms Service and the Ontario Agricultural College. Time of placement and dispersal of colonies within the crops have been shown to be essential factors. A study of the pollen collected by

204 Cornell Univ. Agr. Expt. Sta. Bull. 528, 1931.
205 *Sci. Agr.* 32: 219-225, 1952.
206 *Science* 115: 70-71, 1952.
207 *Canadian Ent.*, in press.
208 Canada Dept. Agr. Bull. 162, 134-157, 1933.

colonies located on specific crops for pollination purposes has provided information on the effect of competing crops; and investigations by R. G. Shuell, Ontario Agricultural College, have clarified the factors affecting nectar secretion.

Teaching and Extension

Apiculture was taught at the Ontario Agricultural College before 1895, but a department was not established until 1908. This is the only institution in Canada that provides a specialized course in apiculture leading to an M.Sc. degree. The Truro Agricultural College, several schools in Quebec, the Manitoba Agricultural College, and the universities of Saskatchewan and British Columbia have provided undergraduate and short courses in beekeeping since their formation.

The provincial apiarists in the various provinces assist in the teaching of the undergraduate and short courses in the winter months; hold field meetings in the summer; organize district associations; carry on beekeeping extension work, aided by their inspectors; and generally act as secretary-treasurers of the provincial beekeepers associations, some of which have been in existence since 1880.

Organizations

The district and provincial associations discuss and make representations for legislation, research, and educational features desired by the industry.

Surplus above domestic demands and lack of export markets led to the formation, by the provincial associations, of three additional honey processing and marketing co-operatives in Manitoba, Saskatchewan, and Alberta in 1939. These were patterned after that in Ontario, which had been in existence since 1924. The procurement of package-bees, queens, beeswax, and equipment became integral parts of these organizations.

In 1940, the provincial associations and the co-operative honey processing plants formed the Canadian Beekeepers' Council to deal with marketing, publicity, extension, research, and all matters of national scope affecting the industry. This close association of provincial organizations, beekeeping supply dealers, container manufacturers, and groups with allied interests forms a well-integrated organization for the beekeeping industry on a national basis.

Legislation

Disease control (American and European foulbrood, etc.) is under provincial administration and acts relative thereto were passed as early as 1914. Federal regulations prohibit importation into Canada of honey bees from any country except the United States, to prevent the spread of the mite *Acarapis woodi* Rennie. Honey bees on combs, used hive equipment, beeswax that has not been liquefied, and honey used as feed in packages or queen cages are prevented from entry to reduce the spread of brood diseases from foreign countries.

Honey grading regulations for export were instituted as a federal measure in 1926 and covered inter-provincial shipments in 1934. Provincial grading regulations were enacted in Saskatchewan in 1947, Manitoba in 1948, Ontario in 1951, and British Columbia in 1952.

Pure food laws, under federal jurisdiction, cover adulteration, net weight, and advertising practices.

Forest Entomology

The development of forest entomology in Canada during the last 45 years parallels, in general, the growth of the forest industries. Demands for lumber, wood pulp, paper, and other specialized products have led to continual growth in the capacity of manufacturing plants and to ever-increasing use of the forests.

Along with the utilization of "weed" species of former years and the exploitation of previously inaccessible forests, there have been marked improvements in standards of utilization and active programs to bring unproductive land back into forest cover. The growth of forest entomology reflects concern, by technical and professional bodies and officials responsible for forest administration, over recurrent outbreaks and timber losses. The major responsibility for forest insect surveys, research, and advisory services has been accepted by the Canada Department of Agriculture. The responsible unit has at successive intervals been designated as the Division of Forest Insects of the Entomological Branch, the Forest Insect Investigations Unit of the Entomology Division, and the Forest Biology Division of Science Service. In this review, it will be referred to mainly as the Division.

This review is concerned primarily with the development of organization of forest entomology, especially within the Department of Agriculture, and the roles of various agencies in this development. Space limitations preclude discussion of technical and scientific contributions; considered evaluation of practical accomplishments, in the sense of protection or control, may appropriately await the passage of time.

Organization in the Department of Agriculture

Serious interest in forest entomology in Canada was first evident in 1909. Several important outbreaks came to the attention of C. Gordon Hewitt almost immediately upon his appointment as Dominion Entomologist in that year. He publicly acknowledged the importance of these problems in December, 1909, before a Select Committee of the House of Commons,[209] and again in January, 1910, when he addressed the Commission of Conservation.[210] He also presented papers to the Canadian Forestry Association and the Manitoba Horticultural and Forestry Association.[211] Hewitt's task of organizing federal government services in all branches of entomology precluded his undertaking personal research in forest entomology, but his interest and authority were important factors in subsequent developments.

J. M. Swaine, appointed in 1912 under Hewitt, was the first Canadian to devote his time continuously to forest entomology. His first major assignment was appraisal of forest insect problems in British Columbia and recommendation of control measures for destructive bark beetle outbreaks in yellow pine stands.[212] Extensive reconnaissance surveys in Eastern Canada were initiated in 1917, and during the following four years vast areas infested by the spruce budworm were surveyed by Swaine, S. A. Graham, C. B. Hutchings, M. B. Dunn, and H. S. Fleming. Aircraft were first used in insect surveys in 1920 and 1921, when Swaine organized budworm surveys in western Quebec and eastern Ontario.[213] Damage surveys were started in 1918, when Swaine co-operated with the Commission of Conservation in intensive plot studies in Quebec,[214] and these were continued by Dunn and Fleming in subsequent years. Parallel studies were initiated at the same time in New Brunswick in co-operation with the N.B. Forest Service, the Forestry School of the University of New Brunswick, and J. D. Tothill of the Natural Control Investigations Laboratory of the Entomology Division at Fredericton. The appraisal and damage surveys of budworm-infested forests in Eastern Canada, and of beetle-infested forests both in the east and in British Columbia, led to an extensive series of biological and taxonomic studies

209 Report of Select Standing Committee on Agriculture and Colonization, House of Commons, Ottawa, 1910.
210 First Ann. Rept. Comm. Conservation, Ottawa, 1910.
211 *Canadian For. J.* 6: 93, 1910; Rept. 16th Ann. Convention Man. Hort. and For. Assoc.: 101-108, 1913.
212 Canada Dept. Agr., Ent. Bull. 7, 1914.
213 *Agr. Gaz.* 8: 20-22, 1921.
214 Tenth Ann. Rept. Comm. Conservation, Ottawa, 1919.

of the Scolytidae and Cerambycidae by Swaine, Hutchings, F. C. Craighead, R. Hopping, G. R. Hopping, E. B. Watson, and L. J. Simpson. Intensive ecological studies of defoliators were initiated by J. J. deGryse in Ontario in the mid-1920's, and were later extended to other parts of Canada.

Experimental application of poison dust from aircraft against the spruce budworm in Cape Breton was studied by Swaine and A. H. MacAndrews in 1927. The technique was tested further by Swaine against the budworm at Westree, Ont., in 1928 and 1929,[215] and against the hemlock looper in Ontario by de Gryse and K. Schedl,[216] in Quebec by Watson,[217] and in British Columbia by G. R. Hopping,[218] from 1929 to 1931. Technical difficulties were overcome in these experiments, and favourable results were obtained against the free-feeding hemlock looper. Results were less satisfactory against the spruce budworm.

With a staff that did not exceed 15 professional forest entomologists and about the same number of sub-professional or seasonal assistants, Swaine had by the late 1920's thoroughly established the foundations of forest entomology in Canada.[219] Many problems had been studied, an extensive number of projects were in operation, and effective co-operative arrangements had been worked out with numerous administrative, technical, and scientific organizations. The service throughout Canada had been consolidated in the Division of Forest Insects within the Entomological Branch about 1914. Territorial responsibilities had been assigned to three laboratories. The Vernon laboratory, established in 1919 to supervise bark beetle control operations in south-central British Columbia, was responsible for surveys and investigations in the two western provinces. The Indian Head laboratory was established in 1923 to deal with insect problems affecting shelterbelts and the parkland area of the three prairie provinces. The establishment of the Forest Insect Laboratory at Fredericton in 1923 coincided with the dissolution of the Natural Control Investigations Laboratory. Its program during the early years included studies of the spruce budworm, bark beetles, and bark and tip weevils.

This territorial organization encouraged the development of forest entomology in British Columbia, the southern part of the Prairie Provinces, and the Maritime Provinces. Staff and appropriations were small, and no further extension of the territorial principle or other major organizational changes occurred during the last 11 years of Swaine's leadership. He and his associates at Ottawa continued to deal with forest insect problems in Quebec, Ontario, and the forested parts of Manitoba and Saskatchewan. The period was marked by extensive surveys, growing use of aircraft, and increased complexity of field ecological investigations.

On the appointment of Swaine as Director of Research in the Department of Agriculture in 1934, J. J. de Gryse took over the direction of the Division. One of the first developments under his leadership was the establishment of the Canadian Forest Insect Survey in 1936. The need for assistance in detecting infestations had been foreseen as early as 1911, when Hewitt described co-operative arrangements with the Forestry Branch.[220] In 1919, Swaine devised report forms for use by field staff of co-operating organizations, and in 1928 he proposed the formation of a "forest insect intelligence service".[221] This proposal was acted upon in 1930 and 1931, when the forest services of Ontario, Quebec, New Brunswick, and Nova Scotia, various limit-holders, and the Dominion Air

215 Canada Dept. Natl. Def., Report on Civil Aviation and Civil Government Air Operations, Ottawa, 1930.
216 *Sci. Agr.* 14: 523-539, 1934.
217 *Sci. Agr.* 14: 669-678, 1934.
218 *Sci. Agr.* 15: 12-29, 1934.
219 Canada Dept. Agr. Pam. 97, 1928.
220 *Canadian For. J.* 7: 35-37, 47, 1911.
221 *Pulp and Paper Mag. Canada* 26(15): 500-502, 1928.

Service assisted the Division in surveys in Eastern Canada, particularly of the European spruce sawfly in the Gaspé Peninsula. By 1935, infestations of the European spruce sawfly, extending from northern Nova Scotia to Ontario in Canada, and from Maine west to New York and south to Connecticut in the United States, were recognized as a serious threat to the spruce stands of eastern North America. A committee to promote co-operation between the forest industry and the Division was set up in 1935 under the auspices of the Canadian Society of Forest Engineers, with de Gryse as initial chairman. The development of specific details for insect surveys in various parts of Canada and of methods to be used in submitting, rearing, and identifying insect samples were among its primary objects.[222] The committee included representatives of the provincial forest services, the Forestry Branch of the Department of Northern Affairs and National Resources, the forest industries, and the Division. In its progress report for 1936,[223] the committee, then under the chairmanship of W. A. E. Pepler, described the intensive co-operative survey of the spruce sawfly in Quebec and Ontario in 1936. Attention was also drawn to the necessity for wider representation on the committee and for extension of the Survey from coast to coast.

The Woodlands Section of the Canadian Pulp and Paper Association became actively interested in forest entomology in 1936. In November of that year A. Koroleff[224] made proposals for strengthening the Survey on a co-operative basis, and suggested the need for additional research, as well as improved instruction at the forestry schools. A special committee of the Woodlands Section under the chairmanship of W. A. E. Pepler accepted these proposals, and prepared a comprehensive plan[225] for co-operative action. It also recommended additional research by the Division and the granting of scholarships by the Association to encourage the training of forest entomologists.

With this combined support of the C.S.F.E. and the C.P.P.A., in addition to that from forest services and protective associations, in 1937 the Survey was intensified in Ontario and Quebec and was extended to the Maritime Provinces and to British Columbia. The volume of material handled in 1937 was about seven times that of 1936. All Survey material was handled in Ottawa headquarters in 1936, but regional units were set up at Fredericton and Vernon in 1937, and subsequently at Winnipeg (1939), Indian Head (1940), Sault Ste. Marie (1945), Calgary (1948), Halifax, and Victoria (1949). In Quebec, the Provincial Bureau of Entomology took over the insect survey in 1939 and has continued its operation to the present time. Insect surveys were started in Newfoundland in 1938 by the Newfoundland Forest Protection Association in co-operation with the Survey unit at Fredericton. After confederation in 1949, intensified surveys were carried out in Newfoundland under the guidance of divisional officers of the Fredericton laboratory. A sub-unit of the Survey was established at Corner Brook in 1952, and this became a fully operative regional unit on completion of the Corner Brook laboratory in 1955.

Decentralization of the Survey through establishment of regional units was, from the beginning, recognized to be important in the proper handling of insect samples and interpretation of regional problems. It was also essential to the creation of an effective organization, which in 1956 comprised 24 research officers, 67 forest biology rangers, and a supporting staff of about 50 members at the nine regional centres; and to the maintenance of essential contacts with some

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222 *For. Chron.* 11(3): 8-11, 1935; 12: 237-239, 1936.
223 *For. Chron.* 13: 327-337, 1937.
224 *For. Chron.* 12: 414-419, 1936.
225 *Pulp and Paper Mag. Canada* 38(1): 24-26, 1937.

2,400 co-operators employed by other organizations. The volume of material handled by the Survey totals some 20,000 or more samples annually. The results are integrated with the program of basic investigations and control projects. In addition to its primary objective of providing information on the occurrence and development of outbreaks of forest insects, the Survey has accumulated extensive data on geographic distribution, biological control factors, life-histories, and habits. Co-ordination and integration of survey projects on a national scale, unification of policies, and standardization of practices wherever feasible are the functions of the Survey Co-ordinator at divisional headquarters. A. W. A. Brown was general director of the Survey from 1936 to 1942 and for the following ten years co-ordination was exercised by the divisional chief. In 1952, B. M. McGugan became co-ordinator of the Survey on a national basis.

For the purpose of this review, only the broad development of the Survey since its conception has been traced. Methods and objectives have been described by de Gryse,[226] and a statement on current trends, projects, and techniques will be presented at the Tenth International Congress of Entomology by McGugan.

Establishment of additional regional laboratories was undertaken by de Gryse concurrently with the development of the Forest Insect Survey. As noted above, this was essential for extension of the Survey on a national basis, and it was equally important in the development of research programs and fulfilment of consultative and advisory services on regional problems. The huge territory that since 1923 had remained the jurisdictional responsibility of Ottawa headquarters was a deterrent to effective work in the forests of northwestern Ontario, Manitoba, and Saskatchewan. This deficiency was brought into prominence by the extensive infestations of the jack-pine budworm in northwestern Ontario and Manitoba in the mid-1930's. To fill this gap a regional forest insect laboratory was established at Winnipeg in 1937, with initial jurisdictional responsibility from Lake Superior to the western boundary of Saskatchewan, and northward to include the Northwest Territories. During the last ten years this laboratory has been the principal centre of studies on the larch sawfly in Canada.[227]

A series of changes affecting divisional organization in British Columbia and Alberta was initiated in 1940. A sub-laboratory had been established at Vancouver in 1925, under the direction of the Vernon laboratory, for attention to problems in the coastal area of British Columbia and for immediate investigations of the western cedar borer. In recognition of the growing importance of forest entomology in the coastal area and the need for close contact with the British Columbia Forest Service, this unit was in 1940 transferred to Victoria and elevated to regional laboratory status. The Vernon laboratory retained regional status for work in the interior of the Province. In 1948, owing to the increasing complexity of the program throughout the Province and the necessity for official contacts with senior officers of the Forest Service, the Victoria laboratory was made the senior divisional establishment in British Columbia. Execution of surveys and of certain field investigations in the interior remained with the Vernon sub-laboratory. In the same year, a regional laboratory was established at Calgary to attend to forest insect problems in the national parks and commercial forests of Alberta and the Northwest Territories, regions that had formerly been within the jurisdictional territories of the Vernon and Winnipeg laboratories.

The divisional program in Ontario was for many years carried out by headquarters staff working directly from Ottawa or from short-term field establishments. In addition to biological studies and chemical control investigations of

226 *J. For.* 36: 983-986, 1938; *Science News* 21: 94-109, 1951.
227 *Canadian Ent.* 87: 111-117, 1955.

the spruce budworm and the hemlock looper, which have already been noted, ecological studies were made of the eastern spruce bark beetle, the European pine shoot moth, the maple leaf cutter, pine sawflies, and the white pine weevil. In 1939, chemical control investigations of nursery and plantation insects were undertaken at Angus in co-operation with the Ontario Department of Lands and Forests. In the early 1940's, increasing severity of insect infestations in Ontario led to negotiations between officials of the Ontario Department of Lands and Forests and the Canada Department of Agriculture regarding increased forest entomological services in the Province. In 1944, a joint agreement was reached, the essence of which as originally set forth and subsequently amended was that the Province would construct and maintain a laboratory at Sault Ste. Marie, to be used by the Department of Agriculture; the latter would staff, equip, and operate the laboratory and conduct insect surveys and field investigations. Problems of regional importance were to be emphasized, but not to the exclusion of fundamental studies of importance to the Division as a whole. Responsibility for control projects and other practical applications was to rest with the Department of Lands and Forests. A joint advisory committee of the two departments was established to study proposals for work program, and to review progress at least once annually. A regional unit was established at Sault Ste. Marie in 1944, and the newly completed laboratory was occupied in 1945. Its jurisdictional territory was northern Ontario, the southern part of the Province being assigned to the newly established Ottawa laboratory. The Sault Ste. Marie laboratory also became the divisional centre for fundamental investigations in genetics and cytology, behaviour, physical ecology and bioclimatology, and insect pathology. The need for specialized facilities for insect pathology was recognized in 1946, and construction of the Insect Pathology Laboratory was started by the Department of Agriculture in 1947. Specialized staff was built up during the following three years, and occupied the laboratory on its completion in 1950.[228]

In the Maritime Provinces notable advances were made during the 1930's and later by the Fredericton laboratory, particularly in studies of the black-headed budworm, the balsam woolly aphid, and the European spruce sawfly. Biological control studies of the last two species have been important laboratory projects. Intensive studies of the virus disease of the European spruce sawfly were initiated in 1940, and investigations of the importance of the disease have been continued to the present time. Among the studies of the birch "die-back", investigations were carried out on the bronze birch borer, the water relations of birch, and the role of climate. Comprehensive studies of the population dynamics of the spruce budworm began in 1944. In that year, a comprehensive program of entomological research and forest management studies was initiated in New Brunswick under the auspices of the Woodlands Section of the Canadian Pulp and Paper Association. This has come to be known as the Green River Project,[229] involving Fraser Companies Ltd., the New Brunswick Department of Lands and Mines, the Forestry Branch, and the Division, each fulfilling its respective functions within the common objective of preventing destructive budworm outbreaks through the application of appropriate management practices.

A unit of the Fredericton laboratory was established at Halifax in 1949 primarily as a centre for insect surveys in Nova Scotia. Another unit with similar functions in Newfoundland was established at Corner Brook in 1952.

For many years the divisional program in the Province of Quebec was carried out by seasonal assignment of members of Ottawa headquarters and

228 *Canada Lumberman* 75(2): 40-45, 1955.
229 *Pulp and Paper Mag. Canada* 56(9): 149, 1955.

the Fredericton laboratory. A study centre for nursery and plantation insect problems, with L. Daviault in charge, was maintained at the provincial forest nursery at Berthierville from 1929 to 1942. The Provincial Bureau of Entomology was formed in 1937, under the direction of R. Gobeil, with the principal object of organizing the forest insect survey in Quebec. An investigational program was also carried out by the Bureau for several years, but this side of its work ceased in the early 1940's. Studies of parasites of the European spruce sawfly in eastern Quebec were carried out by the Fredericton laboratory during the 1930's, and similar studies in the Parke Reserve area were undertaken by the Biological Control Unit of the Entomology Division during the 1940's and early 1950's. Despite these various projects in Quebec, the investigational program was inadequate in view of the great forest wealth of the province and the seriousness of major insect outbreaks. A regional unit of the Division was established in 1952 at Quebec City, in space leased from the Faculty of Forestry, Laval University. The small staff initially available in 1952 has been substantially increased during the last four years, and construction of permanent laboratory facilities is now under way on the university campus.

To complete this summary of important developments under de Gryse's leadership, trends in specialization of work and the formation of the Forest Biology Division warrant brief mention. Fundamental studies were initiated or strengthened at Sault Ste. Marie in 1945 and 1946. In 1950, "sections" were set up for the specialized fields of cytology and genetics, bioclimatology, and insect pathology. The chemical control section, also set up in 1950, was at first a co-operative project of the Division and the Defence Research Board, Department of National Defence. Owing to availability of specialized equipment, facilities, and staff at the Suffield Experiment Station, Defence Research Board, the section was located at Suffield for three years and participated in studies of spray dispersal from aircraft, measurement of deposit, toxicity trials, and field assessment of insect mortality. In 1953, the section was re-located in Ottawa. The essence of sectional organization is freedom from territorial or administrative responsibility, and devotion to research of fundamental importance to the Division as a whole.

In 1951, forest research activities within the Department of Agriculture were consolidated in the newly created Forest Biology Division,[230] by amalgamation of the Forest Insect Investigations Unit of the Entomology Division and the Forest Pathology Section of the Botany and Plant Pathology Division. De Gryse became chief of the Division. In 1952, he retired after 29 years of service to forest entomology in Canada, during 18 of which he gave inspiring leadership and an outstanding demonstration of the fruits of well-conceived co-operative effort. He was succeeded by M. L. Prebble.

During the period 1952 to 1956, advances have been made in the development of joint research projects involving two or more divisional laboratories, and between the Division and other agencies. Disbandment of the Ottawa regional laboratory, which since 1945 had been responsible for the divisional program in southern Ontario, followed the establishment of the Sault Ste. Marie laboratory as the regional centre for the entire province in 1953. Surveys in the Prairie Provinces have been consolidated and strengthened at the Winnipeg and Calgary laboratories. Staffs have been increased in Quebec and Newfoundland, and improvements in laboratory accommodation have been made at Fredericton,[231] Corner Brook, Quebec, and Vernon.

The following is a brief synopsis of successive regional officers-in-charge,

230 *Timber of Canada* 12(6): 36-51, 1952.
231 *Pulp and Paper Mag. Canada* 55(2): 76-78, 80, 82-83, 1954.

current divisional establishments dealing with forest insect problems, and enumeration of the more important insect problems of each region or section.

Ottawa headquarters

Divisional chiefs:—J. M. Swaine, 1912-1934; J. J. de Gryse, 1934-1952; M. L. Prebble, 1952- .

Current staff:—D. E. Gray, Assistant Chief; E. B. Watson, Editor; B. M. McGugan, Survey Co-ordinator, H. Raizenne, Assistant to Co-ordinator; 9 sub-professional and clerical assistants, full-time.

Cytology and Genetics Section (Sault Ste. Marie, Ont.)

Section head:—S. G. Smith, 1950- .

Current staff:—3 research officers; 2 sub-professional assistants, full-time; 5 sub-professional assistants, seasonal.

Important problems:—cytology of Coleoptera and Diprionidae; genetic relationships of budworms of the genus *Choristoneura.*

Bioclimatology Section (Victoria, B.C.)

Section head:—W. G. Wellington, 1950- .

Current staff:—1 sub-professional assistant, full-time (plus 5 research officer colleagues stationed at the Fredericton, Sault Ste. Marie, Winnipeg, and Calgary laboratories).

Important problems:—reactions of lepidopterous and hymenopterous defoliators, and some beetles, to physical factors; studies of microenvironments; investigations of bioclimatological relationships of pest species.

Insect Pathology Laboratory (Sault Ste. Marie, Ont.)

Laboratory head:—J. M. Cameron, 1950- .

Current staff:—12 research officers; 23 sub-professional, clerical, and maintenance assistants, full-time; 10 sub-professional assistants, seasonal.

Important problems:—life-history, morphology, and taxonomy of entomogenous viruses, fungi, bacteria, and protozoa; physiology of host-parasite relationships and studies of pathogenicity; biological control experiments.

Chemical Control Section (Ottawa, Ont.)

Section head:—J. J. Fettes, 1950- .

Current staff:—4 research officers; 1 sub-professional assistant, full-time; 4 sub-professional assistants, seasonal.

Important problems:—investigations of spray dispersal; development of equipment and techniques for laboratory studies of toxicity and for field assessment of control results; chemical control trials against foliage- and root-inhabiting pest species in forest plantations.

Newfoundland

Regional officer-in-charge:—Corner Brook: W. J. Carroll, 1952- .

Current regional staff:—3 sub-professional assistants, full-time; 6 sub-professional assistants, part-time and seasonal.

Important regional problems:—hemlock looper, balsam woolly aphid, larch sawfly, eastern spruce bark beetle, spruce budworm, European spruce sawfly.

Maritime Provinces

Regional officers-in-charge:—Fredericton, N.B.: J. D. Tothill, 1923-1924; L. J. Simpson, 1924-1930; R. E. Balch, 1930- . Sub-laboratory for Nova Scotia: Halifax, 1949-1951, Debert, 1951- , F. G. Cuming, 1949- .

Current staff:—15 research officers; 24 sub-professional, clerical, and maintenance assistants, full-time; 45 sub-professional assistants, seasonal.

Important regional problems:—spruce budworm, balsam woolly aphid, European spruce sawfly, winter moth, bronze birch borer, black-headed budworm, beech scale, fall cankerworm, satin moth.

Quebec

Regional officer-in-charge:—Berthierville: 1929-1942, Quebec City: 1952- , L. Daviault, 1929-1942, 1952- .

Current regional staff:—13 research officers; 20 sub-professional and clerical assistants, full-time; 17 sub-professional assistants, seasonal.

Important regional problems:—spruce budworm, jack-pine sawflies, European spruce sawfly, eastern spruce bark beetle, hemlock looper, forest tent caterpillar.

Ontario

Regional officers-in-charge:—Ottawa: E. B. Watson, 1945-1951; W. H. Haliburton, 1951-1953. Sault Ste. Marie: C. E. Atwood, 1944-1945; M. L. Prebble, 1945-1952; R. M. Belyea, 1952- .

Current regional staff (Sault Ste. Marie):—20 research officers; 47 sub-professional, clerical, and maintenance assistants, full-time; 30 sub-professional assistants, seasonal.

Important regional problems:—spruce budworm, jack-pine budworm, larch sawfly, European pine sawfly, red- and jack-pine sawflies, hemlock looper, white pine weevil, pine root-collar weevil, European pine shoot moth, forest tent caterpillar, maple leaf cutter, eastern spruce bark beetle, cerambycid wood borers, cone and seed insects.

Manitoba and Saskatchewan

Regional officers-in-charge:—Winnipeg: H. A. Richmond, 1937-1945; R. R. Lejeune, 1945-1955; W. A. Reeks, 1955- .

Current regional staff:—9 research officers; 19 sub-professional and clerical assistants, full-time; 11 sub-professional assistants, seasonal.

Important regional problems:—larch sawfly, jack-pine budworm, forest tent caterpillar, spruce budworm, large aspen tortrix, pine tortoise scale, *Hypomolyx* root weevil.

Alberta

Regional officer-in-charge:—Calgary: G. R. Hopping, 1948- .

Current regional staff:—8 research officers; 12 sub-professional and clerical assistants, full-time; 8 sub-professional assistants, seasonal.

Important regional problems:—lodgepole needle miner, mountain pine beetle, spruce budworm, larch sawfly, forest tent caterpillar, *Hypomolyx* root weevil.

Agricultural Area, Prairie Provinces

Regional officers-in-charge:—Indian Head: J. J. de Gryse, 1923-1925; K. E. Stewart, 1927-1939; L. O. T. Peterson, 1939- .

Current regional staff:—2 research officers; 2 sub-professional and clerical assistant, full-time; 3 sub-professional assistants, seasonal.

Important regional problems:—forest tent caterpillar, fall cankerworm, large aspen tortrix, yellow-headed spruce sawfly, pine needle scale.

British Columbia

Regional officers-in-charge:—Vernon: R. Hopping, 1919-1938; G. R. Hopping, 1938-1948; W. G. Mathers, 1948-1955; D. A. Ross, 1955- . Vancouver: G. R. Hopping, 1925-1934; W. G. Mathers, 1934-1940. Victoria: M. L. Prebble, 1940-1945; H. A. Richmond, 1945-1955; R. R. Lejeune, 1955- .

Current regional staff (Victoria and Vernon).—12 research officers; 33 sub-professional and clerical assistants, full-time; 21 sub-professional assistants, seasonal.

Important regional problems:—ambrosia beetles, bark beetles (Douglas fir, mountain pine, Englemann spruce, and others), hemlock looper, spruce budworm, black-headed budworm, Douglas fir tussock moth, Douglas fir needle miner, satin

moth, tent caterpillars, hemlock sawfly, larch sawfly, western cedar borer, cone and seed insects.

Roles of Other Agencies

Most of the advances noted in the preceding section resulted from administrative decisions in the Department of Agriculture and appropriation of funds by Parliament. However, numerous agencies have influenced the course of development of forest entomology through participation in work programs or recommendations to Government. The more important contributions are described in the following paragraphs.

Commission of Conservation

The Commission, set up under the authority of the Conservation Act of 1909, established a number of committees to deal with conservation of natural resources. The Committee on Forests, under the chairmanship of Senator W. C. Edwards, promoted protection from fire, creation of forest reserves, strengthening of the provincial forest services, a program of forest inventories, and research in regeneration and growth of pulpwood stands in the east. The Committee was concerned with insect losses, and heard a submission by Hewitt in 1910; it also included an extensive chapter by Swaine on insect injuries in its monograph *Forests of British Columbia.* Studies of insect damage in Quebec were carried out by Swaine and assistants as part of the investigation of regeneration and growth initiated by forestry staff of the Commission in 1918.

Department of Northern Affairs and National Resources

About 1921, the Forestry Branch of the Department of Northern Affairs and National Resources took over the forest research begun by the Commission of Conservation, and subsequently greatly increased its scope. It maintains district forest offices and experiment stations in various parts of Canada, and has consistently encouraged their use for forest insect investigations.

The Forestry Branch administers the Canada Forestry Act (1949), which provides the basis for integration of research, protection, management, and administration of forest resources, and for co-operation with other federal departments and provincial governments. The provisions of the Act relating to protection of the forests from insects have not as yet been implemented. However, funds have been voted by parliament to share with the Government of New Brunswick and with industry the cost of spraying operations against the spruce budworm in that province in 1953 and later. The Forestry Branch administers this federal contribution to the cost of the spraying operations.

The National Parks Branch and the Northern Administration and Lands Branch assist in insect surveys and research in the areas under their jurisdiction. The Parks Branch has reserved an area for the Eisenhower field laboratory, which serves as the centre for the program of research of the Forest Biology Division in the Rocky Mountain national parks. Direct control operations against the mountain pine beetle in lodgepole pine stands near Banff were carried out by the Parks Branch in 1941-1944, technical direction being provided by the Division.[232]

Department of National Defence

Various agencies of this department have assisted in specific forest entomological projects. The Dominion Air Service provided aircraft for the first aerial surveys of spruce budworm damage in Canada in 1920 and 1921, and for the first experimental dusting operations in infested forests in 1927 to 1929. The Royal Canadian Air Force supplied aircraft for mapping of black-headed budworm

232 *For. Chron.* 21: 98-108, 1945.

infestations in the coastal area of British Columbia in 1944, and for large-scale spraying experiments undertaken by the Ontario Department of Lands and Forests against the spruce budworm in 1945, and by the British Columbia Department of Lands and Forests against the hemlock looper in 1946.

The Defence Research Board co-operated in the early development of the Chemical Control Section, as previously described.

Forest Insects Control Board

Serious and progressive insect damage led, in 1945, to study by the Canadian Pulp and Paper Association of action that might be taken to reduce losses, especially those caused by the spruce budworm. A delegation from the Association presented its views to the Minister of Reconstruction in July, and it was agreed that co-ordination of effort would be desirable under a board responsible to the Minister of Reconstruction. In September, 1945, the Forest Insects Control Board was established by Order-in-Council P.C. 6018 on the recommendation of the ministers of Reconstruction, Agriculture, and Mines and Resources, and with the concurrence of the Cabinet Committee on Reconstruction. The membership of the Board comprised representatives of each of the three above-named departments, the Maritime Provinces, Quebec, Ontario, British Columbia, the Prairie Provinces, and the pulp and paper industry.

The Board was empowered, subject to approval of the Minister of Reconstruction, to take all possible steps, separately and in co-operation with the provinces and industry, to control forest insect outbreaks. It held numerous meetings in Ottawa and other parts of Canada, and carefully considered personnel and financial requirements for improved forest insect surveys and research, as well as direct and indirect control methods. The recommendations of the Board were influential in increasing appropriations and staff for forest insect work within the Department of Agriculture and stimulated the interest of provincial authorities. The Board also proposed that investigations of parasites and diseases of species closely related to the spruce budworm be undertaken in Europe, that a laboratory for the study of insect diseases be constructed in Canada, and that special attention be given to chemical control investigations. These proposals were carried out in due course.

The Board was transferred to the Department of Mines and Resources in 1948, and in 1950 (then under the Department of Resources and Development) it became an advisory board. It continued in this capacity until 1952, when it was disbanded.

Provincial Governments

The provincial forest services are responsible for forest surveys, inventories, reforestation, fire protection, management, and administration. Forest research programs are maintained by several provinces. The provincial forest services participate directly in field activities of the Canadian Forest Insect Survey, and assist the divisional research program by providing facilities at provincial establishments, air and water transportation to inaccessible areas, timber cutting privileges, experimental areas, and building sites. They frequently participate in joint field projects by assigning professional staff, and provide seasonal or sub-professional assistants in entomological projects requiring large field crews. The provincial forest services have taken an active part in the organization of control projects, both small-scale experiments and large-scale commercial operations, including bark beetle control projects in British Columbia in the 1920's, aerial dusting operations in Ontario and Quebec in 1928 and 1929, and aerial spraying operations in various provinces during the last 12 years.

Royal commissions have been appointed to enquire into all aspects of forestry in several provinces during recent years. Briefs on forest entomology were submitted by the Division to the British Columbia Royal Commission in 1944 and to the succeeding commission in 1955; to the Ontario Royal Commission in 1946; and to the Newfoundland Royal Commission in 1954. The reports of the commissioners are valuable because of their comprehensive coverage of all facets of forestry in the respective provinces. In each of the three reports[233] issued to date, the Commissioner took a serious view of forest insect problems, and recommended intensification and integration of efforts to solve them.

Forest Industry

For over 40 years individual firms have provided direct assistance in insect surveys and investigations on company lands, reserved experimental areas, granted cutting privileges, and provided accommodation in company camps. Indispensable as this co-operation at the working level has been, it is through their professional and technical associations that the forest industries have exerted their greatest influence on the development of entomological services in Canada. As already noted, the Canadian Pulp and Paper Association strongly supported the extension of the Forest Insect Survey in 1936 and sponsored the development of the Green River Project in 1944, and made proposals to the Government of Canada that resulted in the establishment of the Forest Insects Control Board in 1945. The Association as a whole and numerous individual pulp and paper and lumber companies provided substantial financial assistance to the Tenth International Congress of Entomology in 1956.

The industry has also strongly supported the four forestry schools in Canada and the establishment of chairs in forest entomology within these schools or in other departments of the universities. Several firms and regional associations have established scholarships open to students specializing in forest entomology. Two scholarship programs on a national basis merit specific mention. In 1938, the Canadian Pulp and Paper Association provided three scholarships each having an annual value of $1,000 for a three-year term for post-graduate training in forest entomology. In 1947, eight forest industries entomological scholarships, each having an annual value of $200 and tenable at the four forestry schools, were established co-operatively by the Canadian Pulp and Paper Association, the Canadian Lumbermen's Association, the B.C. Loggers' Association, and the B.C. Lumber Manufacturers' Association. These have been continued during succeeding years.

The forest industries have taken an active part in direct control operations, in some instances bearing the entire cost, in others sharing the cost with the provincial and federal governments. Among recent control projects organized by individual firms or industrial associations the most noteworthy are control operations against wood-borer damage in Ontario and ambrosia-beetle damage in British Columbia, and the huge aerial spraying projects against the spruce budworm in New Brunswick and Quebec.[234]

Universities

The foremost contribution of the universities to forest entomology in Canada is in the training of research personnel. Instruction in entomology is provided at the four forestry schools (New Brunswick, Laval, Toronto, and British Columbia), and also in the zoology departments of these and about eight other universities.

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233 Report of the Commissioner relating to the Forest Resources of British Columbia, Victoria, B.C., 1945; Report of the Ontario Royal Commission on Forestry, Toronto, Ont., 1947; Report of the Newfoundland Royal Commission on Forestry, St. John's, Nfld., 1955.

234 *Canada Lumberman* 75(11): 34-35, 1955.

At the University of New Brunswick a professorship in forest entomology was established in the Faculty of Forestry in 1939. A. S. West was the first incumbent, and was succeeded in 1946 by N. R. Brown. Postgraduate instruction in forest entomology is provided to the Master's degree.

At Laval University periodic instruction in forest entomology is provided by L. Daviault of the Forest Biology Division. Appointment of a professor in the Faculty of Forestry to look after entomological instruction is expected in the near future.

Professorships in forest entomology were established in the zoology departments of the universities of Toronto and British Columbia in 1945 and 1948 respectively. C. E. Atwood was appointed to the post in Toronto and K. Graham to that in British Columbia. At both universities instruction is provided in forest entomology to the Ph.D. degree.

A number of university staff members undertake research in forest entomology as university projects, or as Forest Biology Division projects during the summer period. Projects of special interest to the Division, but requiring skills or equipment not available at its regional laboratories, are occasionally carried out by university staff with financial support under Department of Agriculture extra-mural research grants.

International Co-operation

For many years forest entomologists in Canada and other countries have exchanged information and collaborated on problems of international importance. Canadian entomologists have gained much from visits to forest insect laboratories in other countries, and from return visits by their foreign colleagues. Such contacts have been especially frequent between Canadian and American forest entomologists. Three international "work conferences", held each year in the eastern, central, and western parts of North America, provide for prompt exchange of information and informal discussion of problems of mutual interest.

American entomologists and foresters have from time to time participated in Canadian forest insect investigations or control projects, with mutual benefit. Officers of the United States Department of Agriculture collaborated in experimental spraying operations against the spruce budworm in Quebec and Ontario, and in the large-scale commercial spraying operations in New Brunswick.

Responsibilities in Forest Insect Control

The predominantly functional basis of forest entomology in Canada emerges clearly from a review of developments during the past 45 years. This is reflected in the interest of the forest industries, the provincial governments, and various agencies of the federal government in economically important problems, and in the distribution of responsibilities in the search for solutions. The Forest Biology Division has the major responsibility for forest insect surveys, research, and consultative and advisory services for Canada as a whole. Other agencies provide substantial assistance to the Division in the execution of this program, and assume more direct responsibilities in the organization and execution of certain types of control projects.

In the use of the biological control method, it is the responsibility of the Division, through its regional laboratories, to assess the need for biological control of a given pest species, and ultimately to appraise the dispersal and effectiveness of any biological control agent that is introduced. This is done as part of the integrated program of insect surveys and ecological research undertaken by the regional laboratories. When insect parasites or predators are introduced from abroad, procurement is the responsibility of the Insect Systematics and Biological

Control Unit of the Entomology Division, or, through the Unit, of the Commonwealth Institute of Biological Control. Propagation, where feasible under laboratory conditions, is undertaken at the Belleville laboratory of the Entomology Division. Studies of initial establishment of introduced parasites and predators are frequently carried out co-operatively by the Division and the aforementioned unit. When disease agents are used in the biological control of forest insects, the Insect Pathology Laboratory is involved in the basic research program and co-operates closely with the regional laboratories in regard to dissemination of the agents of disease and assessment of results. The provincial forest services and the forest industry are not usually involved in financing or administering biological control projects, but they do assist in distribution of the control agent in large-scale projects.

In direct control projects, organization and execution are undertaken by forest industrial firms or associations, the provincial forest services, or the federal government in the case of federal lands. Financing may be undertaken by any one agency, or may be shared by two or three agencies, depending on circumstance. The Division carries out appraisal surveys, studies the ecology and population trends of the pest species, and prepares hazard maps and recommendations for direct control procedures. Close liaison is maintained with the agency responsible for execution of the project, and technical assistance is provided on scheduling and other features of the control operation. The Division also appraises the short- and long-term results of the control program.

For control of forest insect damage through cultural or management practices, there are two basic requirements: first, some modifiable condition of the damaged stands must be recognizable as an important factor in susceptibility; and second, elimination or reduction of the predisposing condition must be economically feasible, and compatible with continued timber production. Forest entomologists in Canada have long been impressed with the potentialities of cultural control,[235] whilst recognizing that the method is apparently not a solution for some of our serious problems. Use of the method depends upon thorough knowledge of the ecology of the susceptible stands and the destructive insect species, and close liaison between the agencies responsible for research, forest regulation, and forest operations. The provincial and federal forest services and the forest industries have a dominant role in the application of cultural control techniques. The Division has similar responsibilities to those described in the preceding paragraph. The most intensive work on the application of cultural control techniques in Canada has been in connection with the spruce budworm problem in the pulpwood forests of New Brunswick. Some of the technical and practical problems encountered in this work have been described by R. F. Morris.[236]

Biological Control

Early colonization and development of Canada and the United States was accomplished by immigration from Europe, and through the channels of settlement, conquest, and commerce many foreign plants and insects gained entrance. Some of these flourished in the new environment and became destructive pests of forest and agricultural crops.

Among the pioneers were competent students of nature, who, noting the importance of natural enemies in regulating the abundance of insects here as in Europe, began transferring these from place to place, thus practising what we know as biological control, or the planned use of beneficial organisms in pest

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235 Canada Dept. Agr. Bull. 37, n.s., 1924; 65th Ann. Rept. Ent. Soc. Ont. (1934): 43-49, 1935; *For. Chron.* 27: 6-37, 1951; *For. Chron.* 31: 314-323, 1955.
236 *Canadian Ent.* 88: 176-181, 1951.

control. Despite difficult and slow communication and travel, early entomologists in North America kept in touch with each other, and the free exchange of information and material begun by them persisted so that we have enjoyed close co-operation between the United States and Canada in this work through the years.

The first use of insect parasites in Canada of which we have official record was that by the eminent entomologist William Saunders, first Director of the Dominion Experimental Farms. As early as 1878, in an address to the Entomological Society of Ontario,[237] he referred to the value of introducing the missing parasites of introduced pests, and in 1882 he obtained from J. A. Lintner, Entomologist of New York State, a supply of the egg parasite *Trichogramma minutum* Riley, which he released to control the imported currantworm, *Nematus ribesii* (Scop.), in Ontario gardens. James Fletcher, appointed the first Dominion Entomologist in 1884, made several introductions of parasites and disease organisms, including further releases of *T. minutum* from the United States and parasites of the hessian fly, *Phytophaga destructor* (Say), from Europe. In this he was given much encouragement and assistance by frequent consultation with L. O. Howard of the U.S. Department of Agriculture, Washington, D.C., a very close friend and one of the great leaders in biological control work.

When C. G. Hewitt was appointed Dominion Entomologist in 1909, he came directly from an investigation of the natural enemies of the larch sawfly, *Pristiphora erichsonii* (Htg.), in England. Although this insect had destroyed most of the larch of merchantable size throughout Eastern Canada, he immediately introduced parasitized material which resulted in colonization of the major parasite *Mesoleius tenthredinis* Morley in southern Manitoba and eastern Quebec.[238] J. M. Swaine assisted in this work and with N. Criddle made the releases in Manitoba.

Hewitt, like his predecessor, had the co-operation of Howard, then Chief of the United States Bureau of Entomology. When the brown-tail moth, *Nygmia phaeorrhoea* (Donov.), invaded New Brunswick and Nova Scotia from the New England States in 1909-1911, important natural enemies introduced and established there at great cost were immediately made available and, through the courtesy of Howard, facilities, equipment, and scientific help of the famed Melrose Highlands parasite laboratory were placed at the disposal of Canada for collection and rearing of parasites and predators.

In 1912, L. S. McLaine was placed in charge of the Canadian work in collecting and rearing parasites of the moth in the United States. J. D. Tothill, who had been appointed the previous year as a field officer in New Brunswick, was in charge of distribution and establishment studies in Canada, with the collaboration of G. E. Sanders, field officer in Nova Scotia, and assisted by A. B. Baird and F. M. McKenzie. Through the courtesy of the University of New Brunswick, a laboratory six by 15 feet was erected on the campus to serve as a receiving depot and study centre and thus became the first biological control laboratory in Canada. By 1916 three important parasites had been established and importation was discontinued. Recovery studies were continued for several years by McLaine, W. N. Keenan, G. P. Walker, P. N. Vroom, L. J. Simpson, F. C. Gilliatt, and others. The parasite *Compsilura concinnata* (Mg.) was recovered from a large number of native species and has since been distributed throughout most of Canada. *Apanteles lacteicolor* Vier. and *Meteorus versicolor* (Wesm.) became very abundant until the brown-tail moth disappeared from

237 9th Ann. Rept. Ent. Soc. Ont. (1878): 4-8, 1879.
238 Report of the Dominion Entomologist, 1909 *et seq.*

Canada but *A. lacteicolor* has not been recovered from any native species. *Calosoma sycophanta* (L.), a very important predator of lepidopterous larvae and pupae, did not become established although released in large numbers in five provinces.

As at Melrose Highlands, the work with introduced parasites stimulated great interest in research on natural enemies and other factors affecting abundance of insects generally, and in 1912 Tothill began investigations on the fall webworm, tent caterpillars, and the spruce budworm, all of which were abundant at that time. Later, work was begun on several other species, including the white-marked tussock moth, the oystershell scale, the cecropia moth, the cherry tortrix, the larch sawfly, the larch casebearer, the Colorado potato beetle, the oak and hemlock loopers, the mourning cloak, and a grass-feeding species, *Ctenucha virginica* (Charp.). As this work developed, there was an ever-increasing overflow from the tiny laboratory to the University Science Building next door and to winter quarters provided on the premises of the New Brunswick Department of Agriculture in Fredericton. In 1915, a brick building with office and laboratory facilities was erected on the University campus by the federal department and named the Natural Control Investigations Laboratory. This laboratory, with insectaries and greenhouses added later, remained the centre for such work until 1922, special studies being carried out at Sylvan Lake, Alta, and Agassiz, Lillooet, and Victoria, B.C., by Tothill and Baird assisted by Vroom and R. Glendenning. A. G. Dustan was a member of the staff for several years and spent much of his time in Nova Scotia, where he initiated use of disease organisms in controlling pests in Canada. Others assisting at Fredericton were Simpson, Vroom, M. B. Dunn, W. P. Addison, A. H. MacAndrews, and R. P. Gorham. Parasites and predators of the oystershell scale were transferred from New Brunswick to British Columbia and an important parasite of tent caterpillars from British Columbia to Alberta. An extensive account of the natural enemies of the fall webworm, *Hyphantria cunea* (Drury), was published,[239] as well as a number of shorter papers dealing with other species.

Natural control investigations were discontinued at Fredericton in 1922. Baird was transferred to Ottawa for taxonomic work, but in the spring of 1923 was assigned temporarily to the Division of Foreign Pests Suppression under McLaine to carry out a program of introduction of parasites of the European corn borer, *Pyrausta nubilalis* (Hbn.), in co-operation with the United States Bureau of Entomology. For this he was established at St. Thomas, Ont., where a large bedroom of his home was transformed into a parasite laboratory, and several hundred thousand parasites were propagated for release. H. G. Dyce, the first assistant in this work, resigned early in 1925 and was succeeded by R. W. Smith. The work was moved in 1925 to Chatham, Ont., where in a seven-room house several million parasites were propagated. Additional staff was employed and other projects were gradually added, including in 1927 redistribution of *M. tenthredinis*, the major parasite of the larch sawfly, and in 1928 introduction of parasites of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westw.), the European earwig, *Forficula auricularia* F., and the oriental fruit moth, *Grapholitha molesta* (Busck).

Farnham House Laboratory in England was founded by the Imperial Bureau of Entomology in 1927, and its services were offered to Canada and other Empire countries in furthering the introduction of parasites and predators and development of the control of pests by biological methods. This led to a conference of senior entomologists in Ottawa in November, 1927, at which

239 Canada Dept. Agr. Bull. 3, n.s. (tech.), 1922.

Howard and a number of other United States entomologists were present in an advisory role. Soon after this a central laboratory for biological control work in Canada was planned. When a suitable location was found in 1929, the staff, equipment and stock of parasites were transferred from Chatham to Belleville, Ont., to establish the Dominion Parasite Laboratory. The staff then included R. W. Smith, G. Wishart, W. E. van Steenburgh, L. J. Briand, A. R. Graham, H. G. James, I. E. Thomas, and others. The property included a 22-room brick house, a barn, and approximately two acres of land. The buildings were remodelled and a three-compartment greenhouse was added in 1930. The projects in hand were expanded more rapidly and introduction of parasites of the wheat stem sawfly, *Cephus cinctus* Nort., was begun.[240] J. H. McLeod, L. R. Finlayson, and H. R. Boyce joined the staff in 1931.

The year 1933 saw the beginning of a new era in biological control with an all-out effort directed by J. M. Swaine to stem a severe infestation in eastern North America by the European spruce sawfly, *Diprion hercyniae* (Htg.). It was a joint effort of forest entomologists, biological control workers, and taxonomists, the United States Bureau of Entomology and Farnham House Laboratory co-operating in obtaining parasites from Europe and the Orient. Federal and provincial government officers, woodland owners and operators, foresters, and farmers collaborated with the entomologists. A 40-room insectary was constructed at Belleville in 1936 with very intricate mechanical quarantine safeguards and with air-conditioning equipment capable of providing all rooms with any temperature and humidity combination required regardless of outside air conditions. Parasites were imported and propagated in millions and distributed through practically every square mile of infested forest in the United States and Canada by men in planes, trucks, automobiles, boats, and canoes and on pack horses and on foot. The campaign was very successful and the introduced parasites, together with a virus disease fortuitously introduced and spread with the parasites, brought the pest under control.

In association with this development, several important additions were made to the staff, including A. Wilkes, G. E. Bucher, J. M. Barclay, T. Burnett, H. C. Coppel, H. L. House, and W. F. Baldwin; and fundamental research, made possible by the improved facilities, was encouraged and developed rapidly.

In the early 1930's, the larch sawfly was discovered in British Columbia and virgin stands of western larch appeared doomed to destruction until the parasite *M. tenthredinis*, collected in Quebec and Ontario and released during 1934-1941, reduced the infestation and prevented serious damage.[241] Subsequently, the parasite was introduced into New Brunswick and Nova Scotia, where it quickly reduced a severe outbreak, and later into northwestern Ontario and the northern part of the Prairie Provinces. The governments of New Brunswick, Quebec, and Ontario assisted in this distribution.

In 1940, Farnham House Laboratory was closed and the Superintendent, W. R. Thompson, transferred to Belleville. With the aid of facilities and services provided by Canada, the service was reorganized and later became the Commonwealth Institute of Biological Control, with a European laboratory at Zurich, Switzerland, and other staff located strategically in several continents. Beginning in 1947, one or more members of the Belleville staff have been in Europe for special assignments in collaboration with the Zurich laboratory, and, through the courtesy and help of officials of many countries, have obtained a large number of beneficial species for Canada.

240 Proc. 5th Pacific Sci. Congr. 1933, 3537-3542, 1934.
241 Proc. 7th Pacific Sci. Congr., 1949, 4: 232-236, 1953.

In 1948, the work was established as the Biological Control Unit with headquarters in Ottawa. Investigations on insect diseases were initiated by Bucher at Kingston, Ont., where facilities were provided by the Department of Bacteriology, Queen's University. Temporary laboratories were established in Quebec City under Briand and at Vancouver, B.C., under McLeod to deal more effectively with urgent local projects. The Belleville laboratory, with A. Wilkes in charge, remained the centre for parasite introduction and propagation and for basic research on problems associated with their use. Wilkes[242] demonstrated for the first time, in his research on *Dahlbominus fuscipennis* (Zett.), a parasite of the European spruce sawfly, that by the application of the principles of genetics it is possible to develop a strain of parasite that has greater fecundity, vigour, and longevity, and to breed in advance races better adapted to the different climates and habitats in which they are to be liberated. Increasing attention has been given to research on basic requirements of insects and studies are in progress in such fields as insect physiology and nutrition, genetics, population ecology, host selectivity, and acclimation. During 1954-1955 the old greenhouse was replaced by two large, modern greenhouses and an attached headerhouse with laboratory facilities. A commodious office and laboratory building[243] was completed in 1955, replacing the old brick house. An isolated wing of this building is completely air-conditioned and houses the pathology section. A separate property of approximately 60 acres some ten miles from Belleville provides facilities for open insectary and field experiments.

Further organizational changes have taken place recently. In 1955, the Biological Control Unit and the Systematic Entomology Unit were amalgamated under G. P. Holland; the staffs from Kingston, Quebec City, and Vancouver are being centred at Belleville again; Wilkes has been transferred to Ottawa for special genetic studies, and B. P. Beirne from Ottawa to Belleville as Officer-in-Charge of the laboratory there. Baird, who has been associated with this work since 1912 and finally as Head of the Biological Control Unit, retires in October, 1956.

In the period 1910-1956, nearly a billion individuals of some 220 species of insect parasites and predators have been released against 68 species of insect pests; and four species of phytophagous insects have been released to assist in the control of the weed St. John's-wort, *Hypericum perforatum* L. More than 50 beneficial species have become established and at least 20 species are important factors in the control of 26 pest species, including, in addition to those mentioned, the European wheat stem sawfly, the pea moth, the holly leaf miner, the apple mealybug, the woolly apple aphid, the satin moth, the European earwig, the greenhouse whitefly, and several species of sawflies attacking pine.

Plant Protection Services

Broadly speaking, plant protection in Canada includes voluntary arrangements such as the comprehensive spray programs developed over 20 years ago in Nova Scotia, Ontario, and Quebec to assist growers in the control of insect pests, particularly those attacking orchards. However, in this section reference is confined to compulsory measures, with emphasis on those under federal jurisdiction. The subject was reviewed by W. N. Keenan[244] in 1937.

Legislation relating to plant protection was enacted under municipal and provincial authority long before national action was contemplated. The earliest preventive measure was the Act for the Preservation of Apple Trees in the

242 Pro. Royal Soc. London, B, 130: 400-415, 1942.
243 *Agr. Inst. Rev.* 10(6): 19-26, 1955.
244 *J. Econ. Ent.* 30: 599-606, 1937.

Parish of Montreal, passed on March 25, 1805, and apparently directed against a cankerworm. Thereafter, legislation aimed specifically at insects was rare until after 1880, when action was taken in various provinces as important new pests appeared, as for example in Prince Edward Island (1883) for the Colorado potato beetle and in Ontario (1898) and Nova Scotia (1898) for the San Jose scale. After 1910, however, legislation was passed in several provinces against insect pests in general: Nova Scotia (1911), New Brunswick (1913), Quebec (1914), Alberta (1922), and Manitoba (1927). Nevertheless, special provincial acts have continued to appear for particularly destructive pests such as grasshoppers in Saskatchewan (1920), the apple maggot in Nova Scotia (1931), and the European corn borer (1925) and the warble fly (1952) in Ontario.

Canada's first national legislation affecting the importation of plant material was the San José Scale Act, passed in 1898. However, the first comprehensive program for examining foreign nursery stock entering Canada was the co-operative arrangement made in 1909 by the Acting Dominion Entomologist, Arthur Gibson, with nurserymen in Ontario and Quebec, arising from the discovery of nests of the brown-tail moth on fruit seedlings imported from France during the early 1900's. The finding in 1909 of 196 nests containing living larvae emphasized the necessity of providing greater protection against the introduction of foreign pests and their spread within the country. Accordingly, in 1910, under the leadership of C. G. Hewitt, the second Dominion Entomologist, the Destructive Insect and Pest Act was passed and the San José Scale Act repealed.

The provisions of the new act were wide, and were phrased with such care that no major changes have been necessary except for amendments made in 1932 and in 1934 to provide for inspection of exports and to clarify the Act in relation to provincial jurisdiction.The Act provided for the Governor General in Council to make such regulations as are deemed expedient to prevent the introduction into Canada or spread therein of any insect, other pest, or disease destructive to vegetation. In summary, the more important original regulations were as follows: —Importations were limited to spring and fall seasons. Nursery stock for propagation, except from Europe, was required to be routed through one of six ports for fumigation, and stock from Japan or the New England States required inspection in addition to fumigation. European shipments required inspection only, and three additional entry ports were, established. Certain greenhouse plants, herbaceous perennials, and bedding plants, bulbs, tubers, etc., were exempted from restriction. A list was given of destructive insects, other pests, and diseases the presence of which on importations would involve entry refusal or treatment; and the responsibility of importers or property owners was stipulated.

Importers were required to inform the Dominion Entomologist of proposed importations. Customs officials co-operated by refusing delivery of importations unless they had been fumigated, inspected, or scheduled for inspection after delivery, and by returning or destroying prohibited shipments. During those early years almost the entire technical staff of the Entomological Branch had to be transferred to plant inspection work during the importing seasons.

The Division of Foreign Pests Suppression of the Entomological Branch was established in 1919 under the direction of L. S. McLaine. The Division, now known as the Plant Protection Division, is responsible for administering regulations under the Act. It was soon realized that in view of the scope of inspection work involved a general reorganization of administration would be required.

Early in 1922 the Destructive Insect and Pest Act Advisory Board was instituted, the personnel being the Dominion Entomologist (Chairman), the Director of Experimental Farms Service (Vice-Chairman), the Deputy Minister of Agriculture, the Dominion Botanist, and the Chief, Division of Foreign Pests Suppression (Secretary). The Board now consists of the Director of Science Service (Chairman) and the chiefs of the divisions of Entomology, Botany and Plant Pathology, Forest Biology, Horticulture, Plant Products, and Plant Protection (Secretary). The Board is not empowered to pass legislation, but may recommend to the Minister of Agriculture for Privy Council approval any changes in the regulations under the Act that are considered advisable and in the public interest.

In 1923 the regulations were revised in regard to importing procedure, and 15 foreign and six domestic regulations established. The important changes were:—An import permit was required for each shipment of nursery stock and of certain plant products; bulbs and perennial and greenhouse plants were made subject to import requirements; inspection and certification were required of all plants in country of origin in addition to inspection in Canada; specific host plants of pests and diseases from certain countries were prohibited or restricted; the importing season was extended to the entire year; new ports of importation were established; domestic regulations were designed to retard or control the spread of pests and diseases within Canada.

Between 1923 and 1949 new regulations were added, and existing regulations revised or rescinded. In 1949 all of the existing regulations were revoked and re-established in consolidated form. A further revocation, consolidation, and re-establishment took place in 1954.

In the reorganization of the Department of Agriculture in 1937 the Plant Protection Division was created by combining the Division of Foreign Pests Suppression of the Entomological Branch with the seed potato certification service of the Division of Botany and Plant Pathology. McLaine remained as divisional chief until his appointment as Dominion Entomologist in 1942, when he was succeeded by Keenan, the present chief. The Division was transferred to Production Service in 1937, to Science Service in 1942, and again to Production Service, April 1, 1956.

The greatly increased volume of imports and the inclusion of additional commodities have necessitated new inspection offices and increased staff. In the fiscal year 1954-1955, nearly 113 million plants were inspected after arrival in Canada as compared to 25 million in 1924-1925. The number of inspections of imported plant products in 1954-1955 was about 1½ times that of 1924-1925.

Scouting, trapping, and eradication projects have been carried on since the earliest days of the Division concerning such pests as the brown-tail moth, the gypsy moth, the European corn borer, Dutch elm disease, oak wilt disease, the Japanese beetle, the San Jose scale, and the apple maggot. Among those who scouted for the brown-tail moth in the Maritime Provinces were: J. D. Tothill, G. E. Sanders, McLaine, A. B. Baird, C. E. Petch, E. H. Strickland, Keenan, A. G. Dustan, P. N. Vroom, and L. J. Simpson. The brown-tail moth is not known to occur in Canada now, and the two known outbreaks of the gypsy moth were eradicated; but, in spite of all efforts, some of these pests have become established in certain areas; yet the delaying action brought about by the control projects has undoubtedly prevented much greater loss.

A field project now being conducted in association with export certification is the inspection of all commercial nurseries during the growing season to check for foreign pests not detected during import inspection.

Before 1932, there was no legislation providing for inspection and certification of exported plant material, although certificates of health were provided when requested by importing countries. That year the Act was amended to correct this situation. This phase of the work has grown rapidly: in 1924-1925, 302 certificates of health were issued to cover exports of plants and plant products, whereas in 1954-1955 the total was 15,487. The Division maintains records of plant legislation of other countries as affecting Canada and provides certificates of health to conform with requirements where possible. To maintain a high degree of insect freedom in plant products examined and certified for export, the Division, in co-operation with the Entomology Division, inspects elevators, grain-storage ships, flour mills, warehouses, and processing plants in which the products are stored or processed. The holds of all ships carrying grain and cereal products to foreign countries are inspected before cargoes are loaded, and fumigation or other treatment if required is supervised by officers of the Division. Fumigation research is conducted with particular reference to the control of insects and diseases affecting living plants and plant products for human consumption.

Through seed potato certification, supplies of high-quality seed are maintained to meet both domestic crop production and an increasing volume for export to many countries. Such certification consists of inspection in the field, in storage, and at shipping point of potato crops entered for certification; and, in co-operation with federal and provincial services concerned, the control of bacterial ring rot of potatoes, the potato-rot nematode, and the potato wart disease. Potato tuber indexing in greenhouses is carried out to assist growers in the development of disease-free seed.

Canada was one of the early signatories to the International Plant Protection Convention approved by FAO in December, 1951. The Convention has among its provisions the agreement of governments to co-ordinate and strengthen legislative measures for the protection of plant resources. In order to prevent, in so far as possible, the spread of insect pests and plant diseases through international trade, the Convention provides for an exchange of information concerning insect and plant disease problems, and requirements or restrictions in plant quarantines. Through the Plant Protection Division, Canada takes an active part in the successful operation of the Convention.

The Division maintains close co-operation with other federal divisions and services in exchange of information and assistance in projects connected with plant protection. The same co-operation exists with regard to provincial governments. In addition to the activities performed in connection with the International Plant Protection Convention, direct contact is maintained with the phytopathological services of many other countries.

Registration and Sale of Insecticides

The first specific legislation concerning insecticides and other pesticides in Canada was the Agricultural Pest Control Act of 1927. This act was designed to standardize the quality of these products and to eliminate from the market those that were not effective for the purposes claimed. Yearly registration was required for each such product sold or offered for sale in Canada, beginning with 1928. In that year 272 brands of pesticides were registered, about 130 being insecticides and about 50 being sulphur dusts, lime-sulphurs, bordeaux mixtures, and oil emulsions.

The original act, after being in force for 11 years, was replaced by the Pest Control Products Act, 1939, under which control was extended to all pesticides used in agriculture, industry, and households. The rather sweeping definition

of *pest control product* is "any produce used, or represented as a means, for preventing, destroying, repelling, mitigating or controlling, directly or indirectly, any insect, fungus, bacterial organism, virus, weed, rodent or other plant or animal pest". Section 10 exempts from the provisions of the Act materials to be used in manufacturing, products that are sold under prescription provisions, and products that are for export only. Yearly registration is still a requirement, and the registration year corresponds to the calendar year. The Act is administered by the Plant Products Division, Department of Agriculture, Ottawa. It is a federal act and there is no comparable provincial legislation.

Since 1950 the control of bactericides has been under the Food and Drugs Act, Department of National Health and Welfare.

The two prime considerations in dealing with an application for registration of a pesticide are: the effectiveness of the product and the safety with which it can be used. The onus of proof rests primarily with the applicant, but Science Service of the Department of Agriculture is the principal consulting agency concerning effectiveness, while the Department of National Health and Welfare is consulted on matters concerning public health. When a product is accepted for registration, a registration number is assigned which is, in effect, the licence for sale, subject to compliance with the labelling requirements.

In 1940, products registered under the revised act numbered 749, of which 487 were insecticides and 15 combination insecticide-fungicides. In recent years, total registrations have increased at the rate of about 300 per year, a greater number than all the registrations for 1928, and in 1955 were 2,875, the insecticides and insecticide-fungicides numbering 1,618 and 164 respectively. This increase in registrations corresponds to the increase in volume and value of pesticides indicated in the yearly reports of the Dominion Bureau of Statistics under "Sales of Pest Control Products". The first of these reports was for the year 1947. The total value in 1947 was estimated at $7,200,000 and in 1954 at $19,700,000, of which approximately half was for insecticides. In 1954 the estimated value of the household and industrial insecticides alone was more than $4,200,000.

Two chemical laboratories of the Plant Products Division, one at Ottawa and the other at Calgary, and a biological pesticide testing laboratory at Ottawa, serve in testing official samples taken by the inspectors in the eight inspection districts in Canada. The increasing number and variety of insecticides now being offered adds to the difficulties in administering the Act. On the other hand, manufacturers are cooperative in adopting the directions for use found to be applicable to Canadian conditions, and in observing the provisions of registration. Recourse to court action for violations has seldom been necessary.

Canada as an Environment for Insect Life[1]

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Contents

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Foreword

Two things make it difficult to write an account of Canada in relation to insect life: the vast size and varied nature of the country and the relatively small amount of work that has been done on its insects. Those familiar with the intensely worked biota of Western Europe or even of many parts of the United States will find this description meagre indeed. In general, Canadian environments are known better than the insects that inhabit them. In only a few orders of insects is our knowledge even of species taxonomy reasonably adequate; for all orders our knowledge of geographical distribution in Canada is sketchy or fragmentary and our knowledge of ecological relations almost non-existent. Serious collecting and study of insects has been carried out in only a few centres. The National Collection itself has been developed actively only since 1919, and on a large scale only in the last few years. There is no close network of amateur and professional workers such as exists in better-studied countries. What I have tried to do, therefore, is to give a brief geographic account of the main environmental factors as seen by an entomologist, to give a short outline of the possible history of the fauna, to give examples of the main distributional types, and to provide a tentative classification of entomological regions, with notes on some characteristic insects of each. The main feature that will undoubtedly be impressed on the reader, as it has been impressed on me, is our ignorance and the need for further investigation of the insect fauna.

I. Physiography

Canada is the world's third largest country. Its area of 3,845,144 square miles is a little greater than that of the U.S.A. and Alaska combined, and nearly as large as that of all of Europe. Canada extends from north to south through 41 degrees of latitude, or about 2,800 miles; its width from Atlantic to Pacific is about 3,000 miles. The mainland is flanked on both east and west coasts by large islands, and on the north by an extensive archipelago. Most regions are well watered, and lakes and streams are abundant; in some areas they occupy a high proportion of the surface (Fig. 1).

The geology of Canada (Fig. 2) has been described in a general article by Alcock (1951) and in a more detailed treatise by Hanson *et al.* (1947). Canada is divided by Alcock into five major geological regions: (1) the Canadian shield; (2) the Appalachian region; (3) the interior plains; (4) the Cordilleran region; and (5) the Northern Arctic folded belt. Basically, the central and eastern

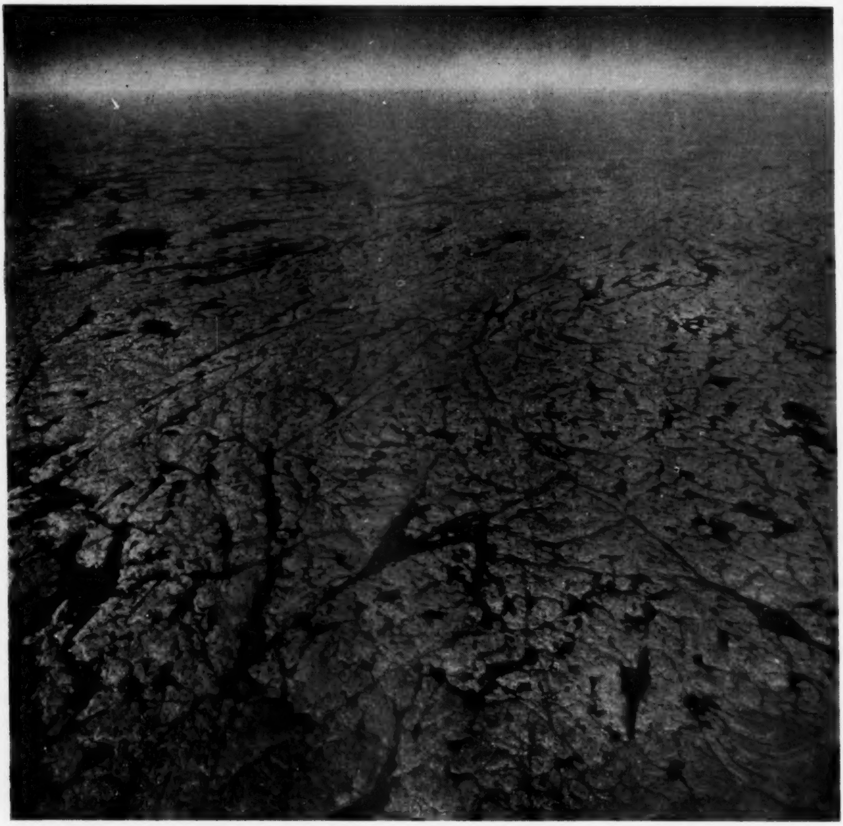

Fig. 1. Aerial view of lakes in northern Canada. R.C.A.F. negative T376L-206, supplied by National Air Photo Library.

Canadian shield of Precambrian rocks is overlapped widely on the west, narrowly on the south, and intermittently on the north by Palaeozoic sediments; the latter are further overlain on the western plains by sediments of Mesozoic and Cenozoic age. The plains are in turn flanked on the southeast, on the west and on the north by the three zones of major folding: the Appalachian region and the Northern Arctic folded belt, in which the main activity was Palaeozoic, and the Cordilleran region, folded in Mesozoic and Cenozoic times.

For practical purposes it is convenient to subdivide Alcock's interior plains region and to group the discordant components of the Arctic archipelago, so as to recognize eight regions: (1) Appalachian region, (2) Canadian shield, (3) St. Lawrence plain, (4) southern Ontario plains, (5) Hudson Bay lowland, (6) interior plains, (7) Cordilleran region, and (8) Arctic Archipelago.

Appalachian Region. The Appalachian chain of folded mountains extends from Georgia northeastward through eastern North America, more or less parallel to the edge of the continental shelf. In Canada it occupies southeastern and extreme southern Quebec, the entire provinces of New Brunswick, Nova Scotia and Prince Edward Island, and the island of Newfoundland. The greater

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Fig. 3.Summit of Mt. Albert, Shickshock Mts., Gaspé Peninsula, P.Q. Reproduced by courtesy of Geological Survey of Canada.

part of the Appalachian region in Canada consists of hills or low mountains with undistinguished relief; however, the northwesterly border of the region in southeastern Quebec is formed by a comparatively high folded chain, culminating in the Shickshock Mountains of the Gaspé Peninsula. Several summits of the Shickshocks reach altitudes of over 4,000 feet, and have appreciable areas above tree-line (Fig. 3).

Canadian Shield. The Canadian shield is one of the world's major areas of resistant Precambrian rock. It extends from Labrador in a broad arc north of the St. Lawrence River and the Great Lakes across northern and eastern Manitoba, northern Saskatchewan and northeastern Alberta into the Northwest Territories, where it occupies the entire mainland east of Great Bear and Great Slave lakes. The rocks of this vast area are mainly igneous, with gneiss and granite predominating, but extensive belts of sediments occur in some places. The height of land in general lies closer to the outer than to the inner boundary of the shield; the highest elevations are found in the east, where the Torngat Mountains of Labrador and the mountains to the north of the lower St. Lawrence River and the Gulf of St. Lawrence reach elevations of 4,000 feet or more (Forbes, 1938). These altitudes are exceptional, and the relief is for the most part low and confused. The contrast between the irregular drainage on jointed, igneous rock and the systematic trend on tilted sediments is well shown on topographic maps (e.g., Dyke Lake and Ashuanipi sheets, National Topographic Series). The weak gradients and irregular topography in a region of plentiful precipitation and low evaporation give rise to extensive systems of bogs, ponds, lakes and streams. The Laurentian shield was completely glaciated and its original soil has been largely scraped off and replaced by shallow soils of post-glacial origin.

St. Lawrence Plain. From Lake Ontario to the Gulf of St. Lawrence the St. Lawrence River follows a nearly straight course through a rather narrow plain which separates the Appalachian from the Laurentian mountains. The floor of this plain is formed of gently sloping Palaeozoic sediments: limestones, sandstones, shales and dolomite. The rocks are overlain by glacial till and by a

considerable range of postglacial marine sands and clays, laid down by the Champlain Sea during the period of isostatic depression immediately following the recession of the ice. Postglacial marine molluscs are found at over 600 feet elevation on Mount Royal, giving an idea of the depth of the general submergence at this time. The plain is broadest in the Ottawa-Montreal region. West of this it is cut off from the southern Ontario plains by a spur of the Canadian shield and by the Adirondack Mountains; to the east it narrows gradually until it is wholly occupied by the St. Lawrence estuary. In the Montreal region the valley floor is pierced by several old volcanic plugs; these form the low but conspicuous Monteregian Hills, which take their name from Mount Royal at Montreal.

Southern Ontario Plains. The plains of southern Ontario are a northeastern extension of the Great Plains of the U.S.A. They are composed of nearly horizontal Palaeozoic sediments overlain by a mantle of glacial till and postglacial lacustrine and alluvial deposits. The plains are divided into a lower easterly and a higher westerly portion by the Niagara escarpment, which extends westward from Niagara Falls to Hamilton and thence northward to Georgian Bay. This region is in general fertile, with flat or gently rolling topography.

Hudson Bay Lowland. This low plain covers a considerable area from south of James Bay northwest to the vicinity of Churchill, Man. Once again nearly flat Palaeozoic sediments are covered by unconsolidated glacial and postglacial deposits. The extremely shallow slope results in poor drainage and extensive areas of boggy land.

Interior Plains. The interior plains of Canada occupy a gradually narrowing truncated wedge, its base nearly coextensive with the southern boundaries of Manitoba, Saskatchewan and Alberta and its apex extending from the Mackenzie delta east to Cape Parry. In Canada the plains lie on three general levels, separated by escarpments. The easternmost and lowest level represents the bed of glacial Lake Agassiz. It includes the general region of lakes Winnipeg and Winnipegosis, and has a mean altitude of about 750 feet. The second level extends diagonally from southwestern Manitoba across Saskatchewan to eastern Alberta, ending near the western tip of Lake Athabaska, where the third level meets the Canadian shield. The average altitude of the second level is about 1,600 feet. The third and highest level, about 2,500 feet in the south, forms a broad belt parallel to the Rocky Mountains all the way from the United States border to the Arctic Ocean. The first level is flat and undissected; the second and third slope gently to the east and north, and have a rolling surface, dissected by deep stream channels or coulees. The drainage of this region is multiple. Near the United States border such streams as the Milk River drain toward the Missouri and Mississippi rivers and ultimately into the Gulf of Mexico. The greater part of the southern or prairie region is drained by the Saskatchewan and Assiniboine rivers into the large lakes of Manitoba and thence through the Nelson River into Hudson Bay. The northern three-fourths of the plains are drained by the vast Mackenzie River (Fig. 4), which, after a course of 2,635 miles, discharges through an extensive delta into the Arctic Ocean.

Cordilleran Region. The southwestern part of Alberta, all but the northeastern part of British Columbia, and the western part of the Yukon Territory are occupied by the ranges of the North American Cordillera, which to the south continues through the U.S.A. to Mexico and Central America and which in its northern part turns westward into Alaska. The geology and topography are too complex to be discussed in detail here, but a map of the main regions is given (Fig. 5); a full account will be found in Bostock (1948). There are two dominant

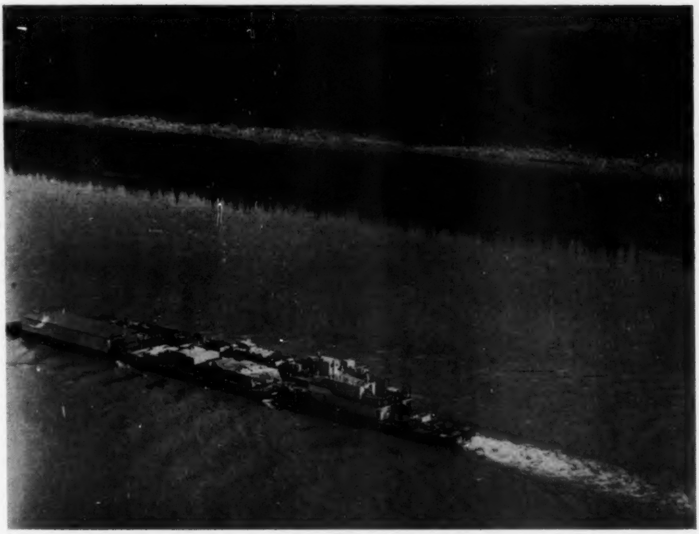


Fig. 4. Mackenzie River, between Wrigley and Norman Wells, N.W.T. R.C.A.F. negative REA 534.5, supplied by National Air Photo Library.

ranges: the Rocky Mountains in the east with elevations of over 12,000 ft., a northward continuation of the mountains of the same name in the U.S.A., and the Coast Range in the west with elevation over 9,000 feet, a continuation not of the Coast Range of Washington, but of the Cascade Mountains of that state. Between the two bounding ranges is an area of considerable relief. In the south this resolves itself into a series of north-south trending ranges and valleys. The most important ranges are the Selkirk and the Gold Mountains; the main valleys are the Kootenay, Columbia and Okanagan. North of this region the Thompson River runs a transverse course, uniting with the longitudinal Fraser River, which turns westward through the Coast Range to empty into the Strait of Georgia near Vancouver. West of the Coast Range, Vancouver Island and the Queen Charlotte Islands form the continuation of the Coast Range of the U.S.A.

Northward the relief becomes increasingly crowded and complex. The parallel ranges of the south are replaced by a high, dissected plateau. The Rocky Mountains are divided by the Liard Valley from the more transversely tending Mackenzie Mountains, which also are high, with altitudes over 8,000 ft. The Coast Range is succeeded by the St. Elias Range, which includes the highest Canadian peak, Mt. Logan, 19,800 ft. (Fig. 6), only 407 feet lower than Mt. McKinley, in the Alaska Range, the highest point in North America. Almost the whole Alaska-Yukon border is mountainous, but it is traversed by the narrow Yukon and Porcupine river valleys, which drain westward into Alaska, and it is flanked on the north by the very narrow coastal strip, important as an extension of the much broader plain north of the Brooks Range in Alaska.

Arctic Archipelago. This region does not form a natural geological unit, but its insular character justifies its separation as a distinct region. Most of the region is an extension of the Canadian shield, and has similar geology and relief. In the east, from Baffin to Ellesmere islands, is a zone of Palaeozoic sediments, forming a mountain chain reaching altitudes of over 8,000 ft. The numerous

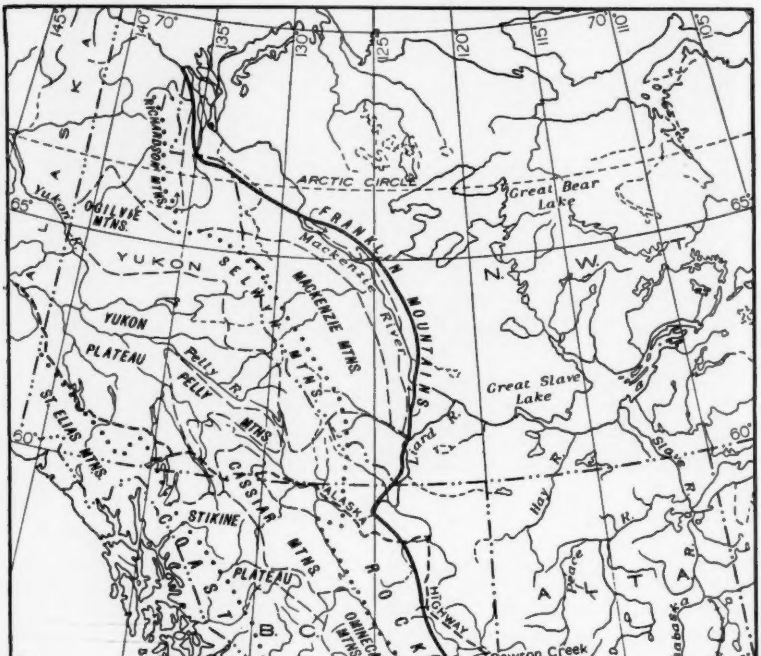


Fig. 5. Physical divisions of the Cordillera region of Canada. Reproduced by courtesy of Geological Survey of Canada.

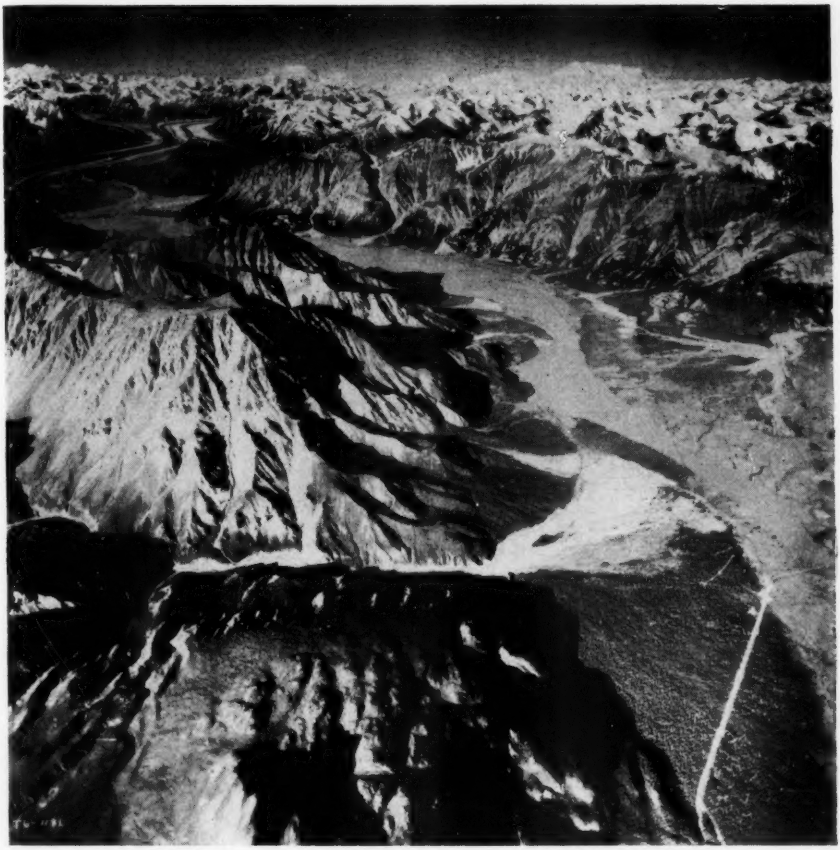


Fig. 6. St. Elias Mts. from the northeast. Mt. Logan, 19,850 ft., the highest mountain in Canada, is the large mountain on the horizon in the right-hand third of the picture. R.C.A.F. negative T6-118L, supplied by National Air Photo Library.

islands form a roughly triangular zone connecting northern Canada with northern Greenland. Taylor (1956) gives an interesting and well-illustrated account of the northernmost islands.

II. Climate

Canada has traditionally been pictured as a land of ice and snow, but actually its climate is extremely varied. There is a wide range from the most rigorous arctic climates to the mild maritime climate of coastal British Columbia, with about the same temperature range as the south of England, to the subarid climates of the southern Okanagan Valley and the Milk River district of Alberta, where cactus and rattlesnakes flourish, and to the warm-temperate climate of southern Ontario, with its oak-chestnut climax forest, and with a fauna and flora much like that of Pittsburgh or Chicago. Good general references on climate are Connor (1949, 1950) and Thomas (1953). Arctic climates are described by Rae (1952).

Fig. 7. Mean annual temperature, Canada (°F.). After Thomas (1953); reproduced by courtesy of Division of Building Research, National Research Council.

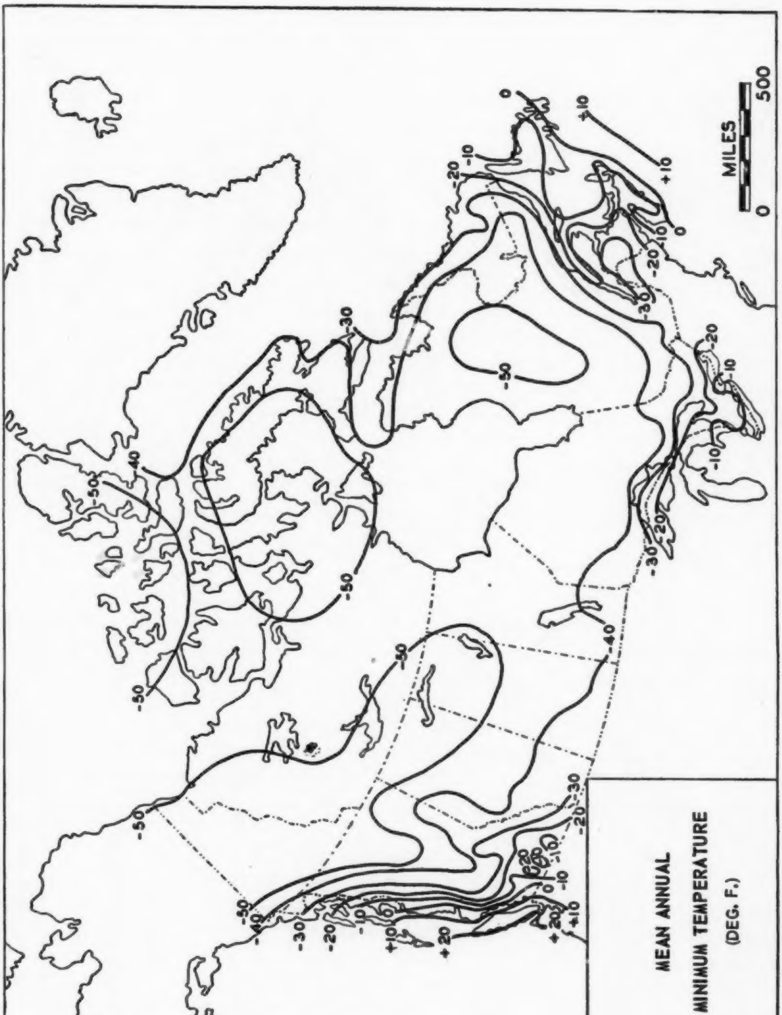


Fig. 8. Mean annual minimum temperature, Canada (°F.). After Thomas (1953); reproduced by courtesy of Division of Building Research, National Research Council.

Fig. 9. Mean annual maximum temperature, Canada (°F.). After Thomas (1953); reproduced by courtesy of Division of Building Research, National Research Council.

Temperature

The distribution of mean annual temperatures in Canada is shown in Fig. 7. The warmest region is on the Pacific coast, in the vicinity of Vancouver and Victoria. Relatively high mean annual temperatures extend to the Alaskan boundary. Another warm zone is found in southern Ontario, the mean annual temperature at Windsor, Ont., being about the same as at Prince Rupert, B.C. The isotherm of 40 degrees Fahrenheit includes almost all of southern British Columbia except for high elevations—not well represented on the map because of the scarcity of recording stations—and two other warm areas: southern Alberta and the Atlantic coastal region of the Maritime Provinces. The 32-degree isotherm includes most of the more densely settled parts of Canada and the main agricultural regions. North of this line the isotherms lie in nearly concentric curves, bending southward in the region of Hudson Bay and sharply northward along the coast of the Atlantic Ocean, Davis Strait and Baffin Bay.

The spatial distribution of temperatures differs appreciably in different seasons, as can be seen from Figs. 8 and 9. The whole interior of the country has a strongly continental climate. Over most of this area differences between mean annual maximum and minimum temperatures are of the order of 135 Fahrenheit or 75 centigrade degrees. The modifying influence of the Great Lakes brings the seasonal difference down to a little more than 100 Fahrenheit degrees in southern Ontario. Similar values occur in the northern Arctic Archipelago and along the east coast as far south as the Strait of Belle Isle. On the southeast coast the differences between mean maxima and minima range from 80 to 100 degrees, and on the Pacific coast they may be as low as 60 degrees. Differences between January and July mean temperatures are of course much smaller, but follow the same general pattern.

Winds

Canada lies within the zone of prevailing westerly winds. The large westerly components are well shown in Fig. 10, which illustrates directional frequencies in summer, the most important period from the standpoint of insect dispersal. There are no remarkable seasonal reversals, though the proportional strength of northerly components is greater in winter and that of southerly components is greater in summer in most localities except on the Pacific coast. Mean wind speeds during the winter show a maximum along the east coast and especially in the region of the Gulf of St. Lawrence, but in summer this maximum tends to disappear and mean wind speeds are surprisingly uniform throughout the country at about 10 m.p.h.

Precipitation

Fig. 11 shows the distribution of mean annual precipitation in Canada. The prevailing westerly winds deposit very heavy precipitation on the abruptly sloping Pacific coast. A minor rain-shadow is formed in the Strait of Georgia and a very pronounced one in the Okanagan Valley. In the Rockies and Selkirks there is a zone of increased precipitation, though the values are much lower than in the coastal zone. The interior plains have comparatively little precipitation; the dryness is accentuated in southeastern Alberta and southwestern Saskatchewan, except for a zone of somewhat higher precipitation in the isolated Cypress Hills. Proceeding northward from the dry area, there is first a small rise in precipitation, followed by a gradual decline, until the lowest values in Canada are found in the northern part of the Arctic Archipelago. The drop in precipitation is counterbalanced, however, by a drop in evaporation as the summer becomes shorter and cooler. The surface of the northern interior, therefore, far from being arid, is wet, and densely studded with lakes and bogs.

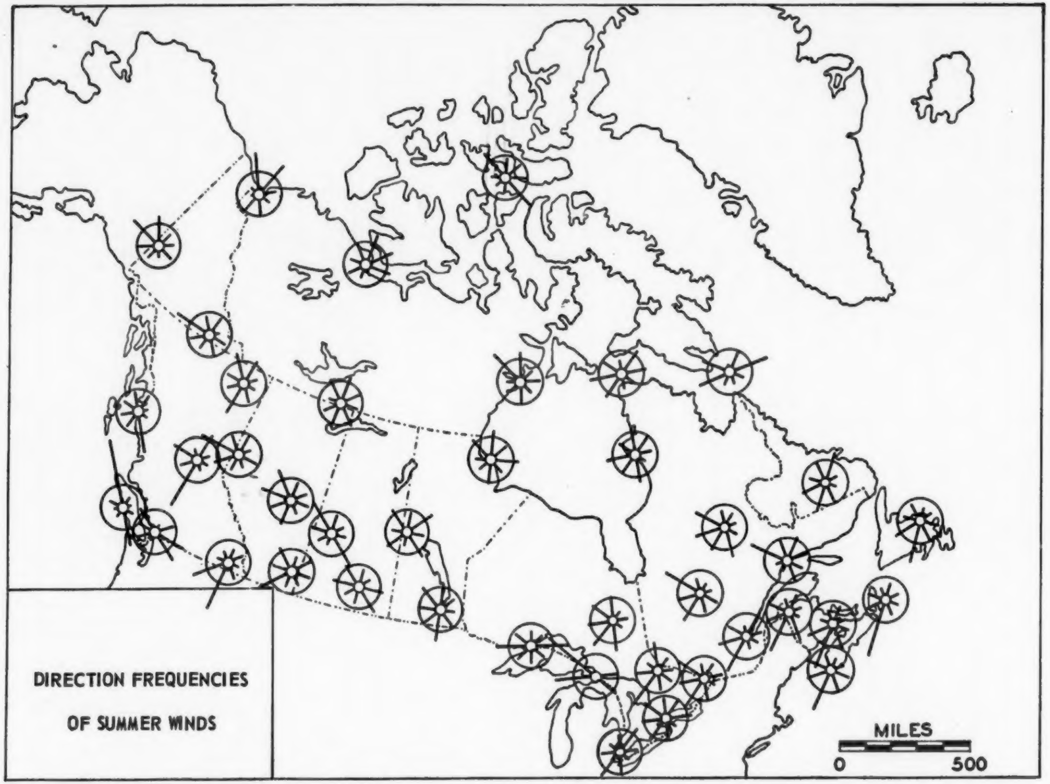


Fig. 10. Distributional frequencies of summer winds, Canada, according to nearest cardinal point of origin. The circle in each diagram indicates 12½ per cent of total records. After Thomas (1953); reproduced by courtesy of Division of Building Research, National Research Council.

Returning to the south, we find that precipitation increases markedly as we go eastward, and the whole of Eastern Canada is a region of fairly high precipitation. As might be expected, there is considerable variation depending on local topography, and there is a maximum along the southeast coast. The highest annual precipitation values in the east are about half the highest values on the west coast.

The seasonal distribution of precipitation is of considerable interest. The dominant feature is of course the partition between rainfall and snowfall. The distribution pattern of rainfall is not greatly different from that of total precipitation, the gradient towards the coastal regions being merely somewhat accentuated by the high ratio of rain to snow in the precipitation. Snowfall, however, has a different distribution (Fig. 12). In the southern parts of the coastal regions the snowfall is comparatively low. The highest regional snowfalls, 150 to 200 inches, are found in the island of Newfoundland and along the Labrador coast. Most of the provinces of Quebec and Newfoundland and a small adjacent part of New Brunswick have a snowfall of 100 inches or more. Restricted belts of heavy snowfall occur to the east of the Great Lakes. Another zone of heavy snowfall is found in British Columbia and the southwestern Yukon. In the northern part of this zone the heaviest snowfalls are coastal, but farther south the warmth of the coastal climate deflects the maximum inland and to higher altitudes. The lowest snowfalls are found (1) in the extreme southwestern coastal zone, where most of the precipitation falls as rain, and (2) in the high Arctic, where the total precipitation is very low.

The seasonal distribution of total precipitation varies with the region. On the east coast there is a late-autumn maximum. The same maximum is much more strongly evident on the west coast. Interior localities have in the southeast and the far north a rather even distribution of precipitation, whereas in medium latitudes and on the western plains they usually show a pronounced summer maximum.

Figs. 13 to 24 are hythergraphs showing mean monthly temperatures and precipitations for 12 Canadian localities of representative climatic types and, for purposes of comparison, the same statistics for Washington, D.C., and London, England.

III. Soils

Stubbe (1951) recognizes five major soil regions: (1) grassland region, (2) forested region (south of the Canadian shield), (3) Canadian shield region, (4) Cordilleran region, and (5) tundra region. The grassland region is divided into three zones: the brown, the dark-brown and the black soil zones. The forested region comprises six zones: the degraded black, the grey-wooded, the high-lime, the grey-brown podzolic, the grey-brown podzolic-podzol transition, and the podzol zones. The Canadian shield region is roughly divisible into a southern zone and a northern or subarctic zone. The tundra region has no major soil divisions. The Cordilleran region has an extremely complex pattern of soils determined by the direct and indirect effects of topography, geology and altitude. The general distribution of these regions and zones is shown on the accompanying map (Fig. 25).

The *brown soil zone* occupies the drier parts of the prairie or southern interior plains. Typical surface soils are brown, thin, and low in organic matter and nitrogen. A lime zone occurs at depths of from six to 12 inches. Poorly drained depressions are usually saline. Solonetzic soils are frequent.

The *dark-brown soil zone* occupies a belt of greater moisture surrounding

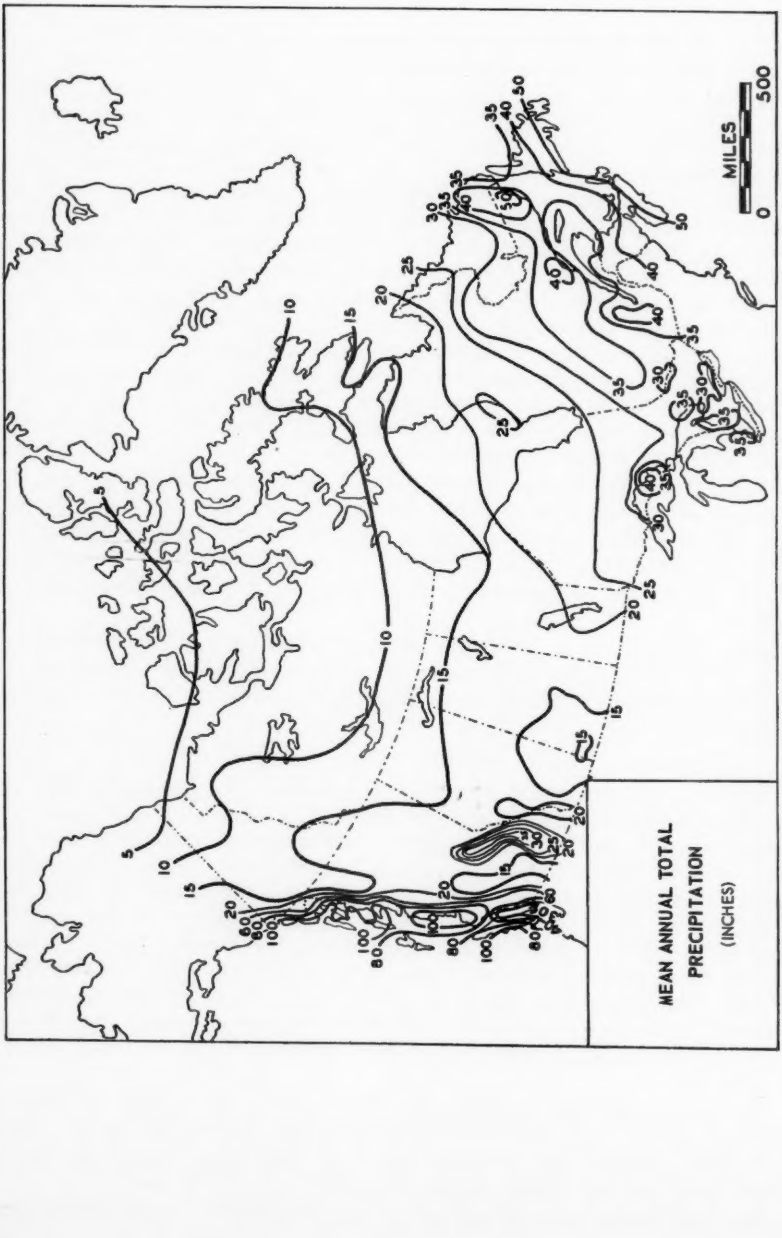


Fig. 11. Mean annual total precipitation, Canada (inches). After Thomas (1953); reproduced by courtesy of Division of Building Research, National Research Council.

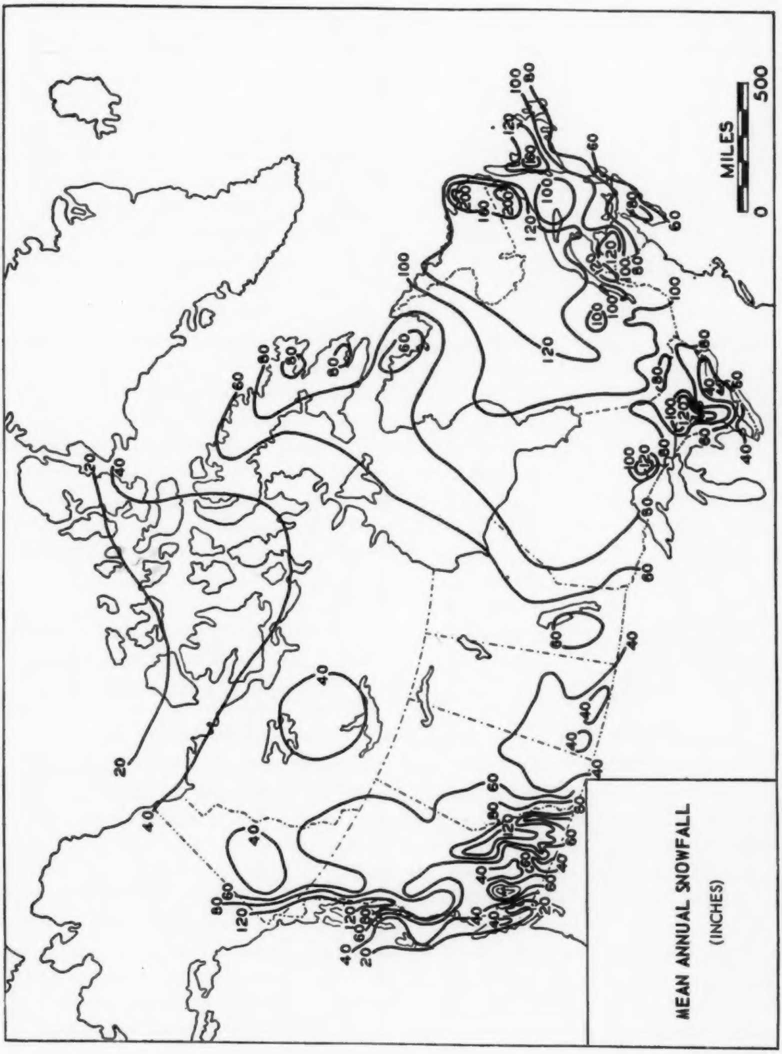
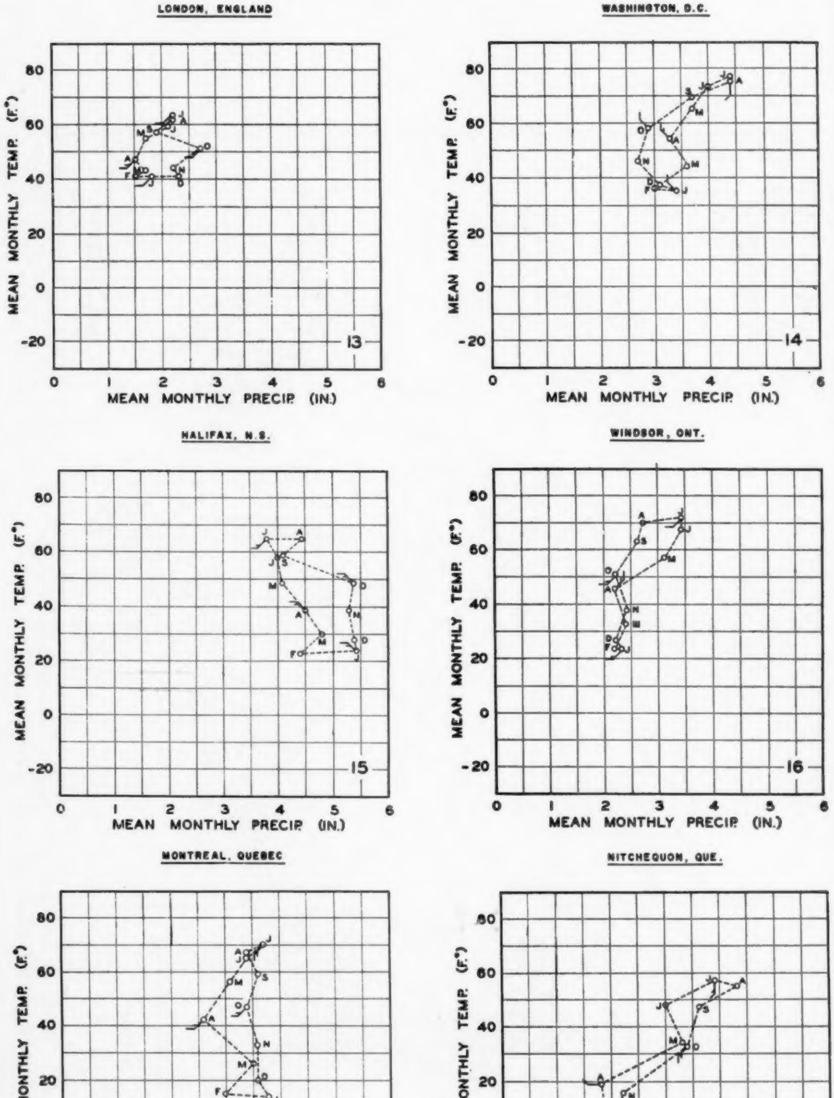


Fig. 12. Mean annual snowfall, Canada (inches). After Thomas (1953); reproduced by courtesy of Division of Building Research, National Research Council.



Figs. 13-18. Hythergraphs for selected localities. After Thomas (1953); reproduced by courtesy of Division of Building Research, National Research Council. Fig. 13, London, England. Fig. 14, Washington, D.C. Fig. 15, Halifax, N.S. Fig. 16, Windsor, Ont. Fig. 17, Montreal, P.Q. Fig. 18, Nitchequon, P.Q.

the brown soil zone. The vegetation is richer and the typical surface soils are dark brown or chestnut-coloured and contain more organic matter and nitrogen than the brown soils. The surface soils are thicker and the lime layer usually occurs at depths of from 10 to 18 inches. Solonetzic soils are fairly common and saline soils are often found in depressions.

The *black soil zone* is peripheral to the dark-brown soil zone and has a moister climate and richer vegetation. Typical surface soils, four inches to two feet deep, are very dark brown or black and are rich in organic matter and nitrogen. The lime layer generally occurs at depths of 18 to 36 inches. Solonetzic and saline soils are less common than in the brown and dark-brown soil zones. Depressions may be tree-covered and have a grey surface soil; such soils are called "depression" or "slough" podzols.

The *degraded black soil zone* is a transition between the preceding and following zones. Soils vary locally from typical black to typical grey-wooded compositions; most are in an intermediate grey-black category. Depressions contain podzols or peat. Solonetzic soils occur locally.

The *grey-wooded soil zone* occupies most of the forested part of the interior plains. It is formed under an annual precipitation of 12 to 22 inches and a cover of conifers mixed with popular and willow. The dominant soils have a thin surface layer of dark leaf-mould, below which is a layer of light-grey soil. There is a layer of lime accumulation at 24 to 48 inches. Depression soils include podzols, peat and muck. Solonetzic soils occur locally. The soils of this zone are less fertile than those of the zones previously discussed.

The *high-lime soil zone* occurs in large areas of Manitoba and limited areas of Saskatchewan characterized by calcareous bed-rock and highly calcareous glacial drift. The soils vary considerably, and show north-to-south zonation. In the south there is a shallow black layer of granular and friable soil over a marly, crumbly layer of lime accumulation. In the northern part of the zone, with greater moisture effectivity, there is some degradation of the surface, and there is a whitish-grey leached zone beneath the leaf-mat, underlain by a darker layer, which in turn is underlain by a marly layer of lime accumulation. A number of local variations are discussed by Ellis (1938).

The *grey-brown podzolic soil zone* exists in southern Ontario in a humid climate and under a deciduous or mixed forest cover. Typical well-drained soils have a greyish-brown, mildly acid surface soil, a brown, somewhat heavier sub-surface layer and a limy, greyish subsoil. Texture is variable. Imperfectly drained soils belong to the dark-grey gleisolic soil type. They are darker in colour and lack the brown sub-surface horizon. Black muck and peat occur in poorly drained depressions. The fertility of these soils is good, though not equal to that of the best soils of the grassland region.

The *grey-brown podzolic-podzol transition zone* occupies the lower Ottawa River valley and the western part of the St. Lawrence plain. The most important soils are of the dark-grey gleisolic type; they are usually heavy and imperfectly drained. There are a large number of other soil types depending on local conditions. Among these are grey-brown podzolic and brown forest soils on calcareous materials, especially in the western part of the zone, brown podzolic and podzol soils on lighter, non-calcareous, and especially sandy, materials, and black-muck and peat soils in poorly drained depressions.

The *podzol zone* comprises southeastern Quebec and the Maritime Provinces with the exception of Newfoundland, and is associated with coniferous or mixed forest. The typical well-drained soils are podzols, with a light-grey or white

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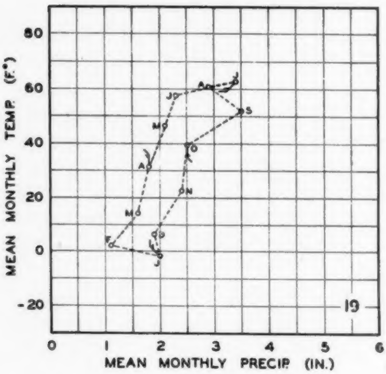

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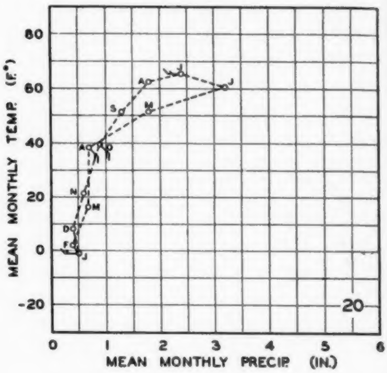

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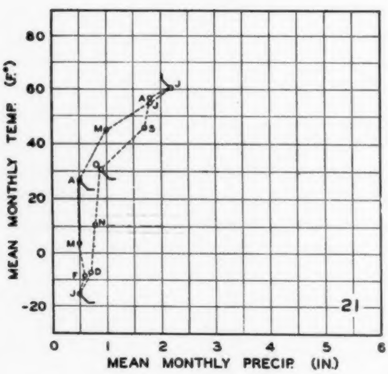

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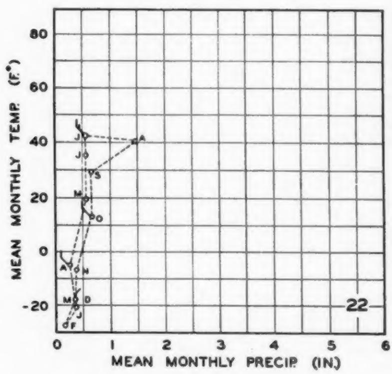

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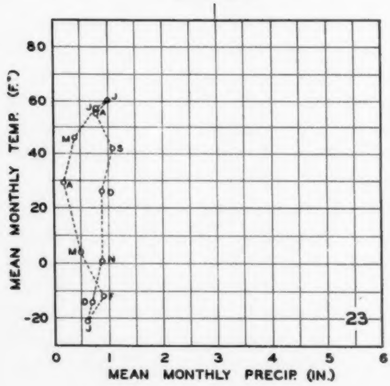

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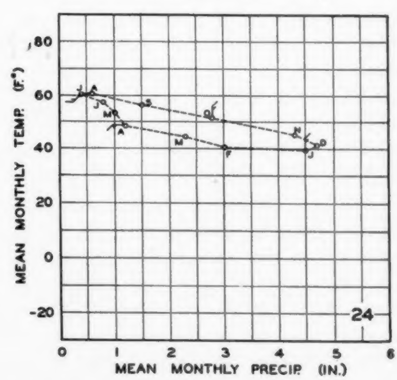

Figs. 19-24. Hythergraphs for selected localities. After Thomas (1953); reproduced by courtesy of Division of Building Research, National Research Council. Fig. 19, Kapuskasing, Ont. Fig. 20, Regina, Sask. Fig. 21, Fort Smith, N.W.T. Fig. 22, Arctic Bay, N.W.T. Fig. 23, Dawson, Y.T. Fig. 24, Victoria, B.C.

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leached layer immediately under the leaf mat. Under cultivation the surface soil is usually reddish or greyish brown. Poor drainage may result in increased leaching and a thicker light-grey horizon, or decreased leaching and a dark surface soil. Poorly drained depressions are often occupied by peat, seldom by black muck. The soils of this zone are of rather low fertility and are of moderately to strongly acid reaction.

The *southern division of the Canadian shield region* in general has a thin covering of unconsolidated soil material over resistant bedrock. Areas of naked rock outcrop are frequent. Peat and swamp occupy extensive depressions. Brown podzol and podzolic soils occur on the upland. There are extensive smooth clay plains in the Clay Belt of eastern Ontario and western Quebec; better-drained soils in this belt resemble the grey-wooded soils, but a large proportion of the soils are poorly drained and covered by a thin layer of peat.

In the *subarctic division of the Canadian shield region* the proportion of peat and swamp is greater; a large part of the soils are underlain by permafrost. In upland areas true soils are often virtually absent, unaltered mineral material being covered by a thin layer of moss and lichen.

The *tundra region* has permanently frozen subsoils at shallow depths and only a short period of superficial thawing in the summer. Organic deposition and chemical weathering are minimal, but frost comminution and solifluction are very active. Polygon and stripe formations, frost-domes, etc., are prominent features, and mechanical disturbance of the soil has an important influence on plant life.

The *Cordilleran region* is, properly speaking, a complex of altitudinal and geological zones, many of whose individual components closely parallel typical soils of other regions. In the dry southern valleys, under grassland conditions, brown, dark-brown and black soils are found, comparable to those of the prairies; at higher elevations, under forest cover, podzols are found (Kelley and Spilsbury, 1949). Spilsbury and Tisdale (1944) describe three podzol zones in this region. The correlation between vegetation and soil zones is close. The zonal and altitudinal relations are as follows:—

Altitude, ft.	Soil Zone	Plant Zone
1100-2300	Brown Earth	Lower Grassland
2300-2800	Dark Brown Earth	Middle Grassland
2800-3200	Black Earth	Upper Grassland
3200-4000	Lower Podzol	Montane Forest
4000-4800	Middle Podzol	Subalpine Forest
4800-6100	Upper Podzol	Upper Subalpine

Farther north in the interior, Farstad and Laird (1954) recognize five principal soil types: degraded black, grey wooded, brown podzolic, podzol, and podolized grey wooded. The degraded black soils characterize isolated grassland areas, here near their northern geographic limit; grey wooded soils are characteristic of uplands of the interior plateau; brown podzolic soils are formed under the influence of a humid Pacific climate, and show certain differences from soils of the same class in the east; podzols are found in humid sections on areas of sandy and gravelly low-lime parent material under coniferous forest cover; podzolized grey wooded soils occupy an intermediate position between podzols and grey wooded soils. Other soils found under special conditions are: bog, half bog, dark-grey gleisolic, groundwater podzol, and alluvial soils. On the Pacific coast brown podzolic soils are characteristic. These are shown on the map as Pacific coast soils. Northern and high-altitude soils in the Cordilleran region have not been thoroughly studied.

IV. Vegetation

The study of North American vegetation has been much influenced by the climax theory (Clements, 1904, 1916, 1936; Phillips, 1934-35; Shelford, 1932), and regional vegetation has usually been characterized in terms of real or supposed climax associations. Although this theory has been extensively criticized in recent years on the ground of artificiality (Cain, 1939; Gleason, 1939; Hutchison, 1941; Nichols, 1929; Tansley, 1935; Whittaker, 1953), nonetheless it provides a simple basic framework for the arrangement of the complex details of plant distribution, one that is perhaps particularly useful in a region such as Canada, where very large areas of fairly uniform vegetation occur, often giving way to other extensive vegetational areas at a sharp boundary or in a narrow transition zone. Although the climatic climax may be a reality, ecologists increasingly recognize that under many conditions the climax may never be reached, or at any rate not until changes in topography or substratum have been accomplished that would take far longer than the probable duration of a stable climate and vegetation in the region. On different land-forms or mineral substrates different reasonably stable associations may be formed. Whether these are thought of as subclimaxes tending towards a single climatic climax or as co-ordinates in a polyclimax theory is hardly more than a difference in terminology.

Apart from stable and natural climaxes or subclimaxes, two other types of vegetation are important in Canada: seral stages, i.e., successional communities, and vegetation disturbed by man or by fire. Seres will be discussed in more detail under the vegetational regions. Disturbance by man is of two general types: destruction of native vegetation and introduction of alien species. Destruction may be total as in paved or built-up areas, or nearly so as in thoroughly cultivated lands, where only a few weed species retain a foothold. Often, however, the native vegetation is disturbed rather than destroyed: forest composition is altered by selective cutting, or forest is replaced by early seral stages or by a grazing disclimax. Though the destruction of native vegetation is not as great as in either Europe or the United States it is nonetheless very severe in southern Canada. In the east, large areas of forest have been replaced by open ground; over the settled parts of Ontario, Quebec and the Maritime Provinces areas of virgin forest are comparatively rare, though there are extensive tracts of second growth and of forest modified by cutting. On the prairies much of the best land is under cultivation to wheat and other crops; large additional areas are greatly modified by grazing. In British Columbia the grasslands of the interior valleys have been modified by grazing and have been partly displaced, especially at lower elevations, by orchards and other cultivated lands. Lumbering has had a strong influence on forests in the southern half of British Columbia, but has so far been less important in the northern part of that province and indeed of Canada in general. Fires can be started by natural causes, but their frequency increases greatly with human occupancy. Not only are fires primarily destructive but they also inhibit reproduction, especially in forests, as has been shown by Candy (1951). On prairie, burning depresses productivity only for a year or so (Aldous, 1934).

Introduced plants are of two main classes: those deliberately introduced under cultivation and adventive species accidentally brought in. Cultivated plants usually grow only under protected conditions; only a small proportion of the species become naturalized, even under disturbed conditions. A considerable number of better-adapted plants have been introduced accidentally. Few of

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these succeed in breaking into established climax vegetation, but in disturbed sites they are numerous or even predominant. Of 195 species of weeds listed by Frankton (1955), 116 are introduced. About 25 per cent of the 1,000 dicotyledons listed by Marie-Victorin (1935) for Quebec are introduced, mostly from Europe or Eurasia. Almost all of these are characteristic of cultivated, waste, or abandoned land, only about 30 species appear to compete freely in undisturbed sites. Animals appear to enter native associations with somewhat greater ease: the Hungarian partridge appears to survive on essentially wild prairie, the carp is well established in the St. Lawrence drainage, and many introduced species of insects are firmly established on native plant hosts, some playing a major part in climax associations, e.g., spruce sawfly, *Diprion hercyniae* (Htg.) and European pine shoot moth, *Rhyacionia buoliana* (Schiff.)

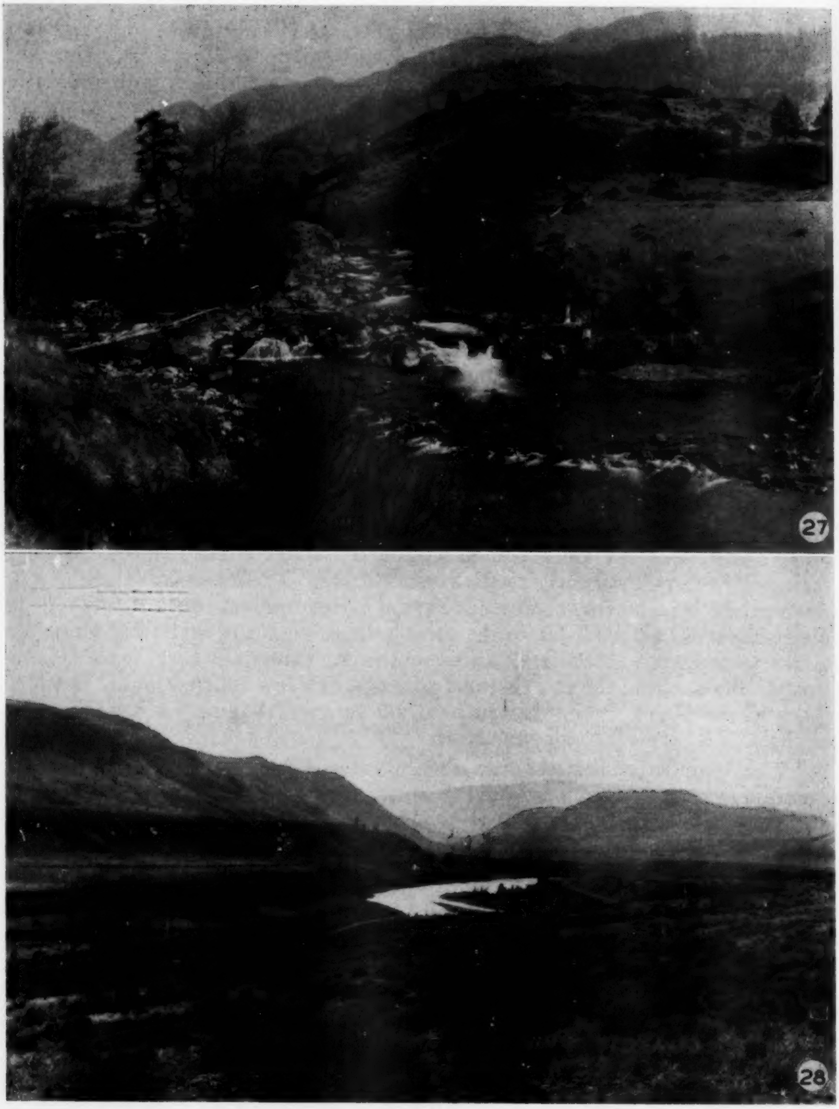
The climax vegetation of Canada falls into four major types or formations,[1] distinguished by the life-forms of their dominant plants (Fig. 26). These are: grassland, deciduous forest, coniferous forest, and tundra. Each of these zones is divisible into vegetational regions. In the tundra an ecological classification does not yet seem possible, and the division is mainly biogeographic. In the other formations the main division is based on the apparent distribution of climax associations. The general distribution of the formations is determined by climate. Grassland climaxes occur in the warm rain-shadow areas of Western Canada, viz.: the plains north of the United States border and the interior valleys of British Columbia. Deciduous forest occurs in the warm moist areas of southeastern and southcentral Canada. Coniferous forest extends in a broad belt from coast to coast north of the deciduous forest and grassland zones, going south along the Cordillera to the United States border, and north along sheltered river valleys nearly to the Arctic Ocean. Tundra occupies the Arctic Archipelago and extensive areas along the north and northeast coasts of the mainland; tundra extends far to the southward at gradually increasing elevations in the mountains. In the west these southward extensions form a fairly continuous chain, but in the east they are confined to a few isolated peaks, of which those in the Gaspé Peninsula, Quebec, and mounts Washington and Katahdin in the U.S.A. are the most important.

The boundaries between the formations are usually occupied by broad transitional areas or ecotones — the "hemiarctic" of Ungava, the aspen parkland of Western Canada, and the pine-hemlock-northern hardwoods forest of the east — but sometimes the boundary is sharp and without transition, as between coniferous forest and tundra at Churchill, Manitoba.

Grassland Formation

The grassland formation of Canada falls into two geographic divisions: the prairies, occupying the southern part of the interior plains, and the interior valleys of British Columbia. The grassland of British Columbia is most conveniently referred to a single region, the palouse grassland, though it comprises three altitudinally limited associations (Tisdale, 1947). The prairies of Canada are divisible into three regions (Coupland, 1952): the true prairie region in a part of southern Manitoba; the mixed prairie region, occupying much of southern Alberta and Saskatchewan; and the fescue grassland region, occupying a peripheral zone around the western and northern borders of the mixed prairie region, and entering as a grassland component into the aspen parkland zone, described under the coniferous forest formation, below. Thus four of the seven grassland regions of North America are represented in Canada.

1Halliday (1937) distinguishes three formations, uniting the deciduous and coniferous forests; Weaver and Clements (1938) rank as formations some units that here are termed associations.



Figs. 27-28. Fig. 27, Upper Palouse grassland, Okanagan Falls, B.C. Science Service. Fig. 28, Lower Palouse grassland, with *Artemisia tridentata*, Walhachin, B.C. Science Service.

Palouse Grassland Region

This region of Canada is the northern extension of the much larger intermontane grassland area of the northwestern U.S.A. In Canada the palouse grassland is confined to rather narrow lake and river valleys and has a restricted and partly discontinuous distribution governed by the arrangement of these. Tisdale distinguishes three zones: the lower grassland, the middle grassland, and the upper grassland; these are associated with different soils and have distinct climax and subclimax vegetations.

The *lower grassland* occurs on brown-earth soils at elevations from 1,200 to 2,300 ft. (Fig. 27). Mean July temperatures range from 70° to 74°F., mean annual precipitation from seven to ten inches. This zone is characterized by abundance of perennial bunchgrasses and xeric shrubs. The climax dominants are *Agropyron spicatum* (Pursh) Scribn. & Sm. and *Artemisia tridentata* Nutt. With overgrazing, *Artemisia* increases and an associes dominated by *A. tridentata*, *Poa secunda* Presl and *Antennaria dimorpha* (Nutt.) T. & G. develops. This associes is highly xeric in appearance (Fig. 28), and contains *Opuntia fragilis* (Nutt.) Haw. and other xerothemic plants. An edaphic community on coarse soils is dominated by *Stipa comata* Trin. & Rupr., *Sporobolus cryptandrus* (Torr.) Gray, and sometimes by *Chrysothamnus nauseosus* (Pall.) Britt. This community occupies a much less extensive area than the climax community.

The *middle grassland* occurs on dark-brown-earth soils at elevations of from 2,300 to 2,800 and occasionally to 3,400 feet. Mean July temperatures are of the order of 67°F., mean annual precipitation is about 12 inches. The climax vegetation is dominated by *Agropyron spicatum* and *Poa secunda*. This vegetation differs from the lower grassland climax in the insignificance of *Artemisia tridentata*, in the comparative abundance of *Artemisia frigida* Willd. and *Antennaria dimorpha*, in the common appearance of *Koeleria cristata* (L.) Pers. and *Antennaria parvifolia* Nutt., and in the presence in insignificant numbers of *Festuca scabrella* Torr., *Balsamorhiza sagittata* (Pursh) Nutt., *Achillea millefolium* L. var. *lanulosa* (Nutt.) Piper and *Crepis intermedia* Gray. Overgrazing has given rise to two associes. The *Stipa-Agropyron-Poa* associes is the most extensive community in the middle zone at the present time. It is dominated by *Stipa comata*, with *Agropyron spicatum* and *Poa secunda* present but much reduced in importance, and with annuals such as *Bromus tectorum* L. and *Lappula occidentalis* (S. Wats.) Rydb. increased in importance. The *Bromus-Poa-Stipa* associes develops from the *Stipa-Agropyron-Poa* associes with continued overgrazing. It is unusual in being dominated by an introduced species, *Bromus tectorum*, and has developed since the arrival of this grass about 1920. It occurs in scattered patches of up to a few square miles in extent, but occupies a considerable aggregate area in the zone.

The *upper grassland* occurs on black earth or chernozem soils, at elevations from 2,700 to 3,300 and occasionally to 4,000 feet. July temperatures are about as in the middle grassland zone, but the precipitation is higher, around 15 inches a year. The climax vegetation is dominated by *Agropyron spicatum*, with *Festuca scabrella* an associate of locally variable importance. *Koeleria cristata* is important and *Carex praegracilis* W. Boott is common. The vegetation is richer in species than in the middle zone and much richer than in the lower zone. Undisturbed climax communities are now rare. Two associes developed by overgrazing occupy most of the zone. The *Stipa-Poa* associes, dominated by *Stipa columbiana* Macoun and *Poa pratensis* L., is the more extensive. *Stipa* is ascendant over *Poa* on coarse soils and exposed sites; *Poa* is favoured by fine,

deep soils. The *Poa-Bromus* association is produced by severe overgrazing. The principal dominant is *Poa secunda*, with *Bromus tectorum* locally variable in importance.

Mixed Prairie Region

This region (Fig. 29) covers most of the southern part of the plains in Alberta and Saskatchewan. It occupies the entire brown soil region and extends a considerable distance into the drier part of the dark-brown soil region. Mean annual precipitation ranges from about 11 to about 13.5 inches, mean annual temperatures from 38.5 to 40.7°F. Frost-free days per year range from 108 to 126.

Coupland (1950, 1952) has studied the ecology of this region in considerable detail. He recognizes five climax communities or faciations: (1) *Stipa-Bouteloua* faciation; (2) *Bouteloua-Stipa* faciation; (3) *Stipa-Agropyron* faciation; (4) *Agropyron-Koeleria* faciation; and (5) *Bouteloua-Agropyron* faciation.

The *Stipa-Bouteloua* faciation is by far the most extensive. It characterizes medium textured soils in the moister part of the brown soil zone and the drier part of the dark-brown soil zone. The dominant species are *Stipa comata*, *Stipa spartea* Trin. var. *curtiseta* Hitch., and *Bouteloua gracilis* (H.B.K.) Lag. There are three layers of vegetation: an upper layer, at five to 20 inches from the ground, consisting of mid-grasses and flowering stems of forbs; a middle layer, at one to five inches, consisting of *Bouteloua gracilis*, *Carex eleocharis* Bailey and shorter forbs, such as *Phlox hoodii* Richn. and *Malvastrum coccineum* (Pursh) Gray. The third layer, up to one inch above the surface is composed of *Selaginella densa* Rydb. Shrubs occur in areas of deep moisture penetration, e.g. in sheltered positions on coulee slopes; the most common species are *Symphoricarpos occidentalis* Hook., *Rosa* spp., and *Elaeagnus commutata* Bernh. Dominant, principal and secondary species include 15 species of grasses, four of sedges, 28 of forbs, one shrub and one clubmoss. An additional 40 species of forbs, three of shrubs and two of half-shrubs are sufficiently numerous to be considered characteristic of the type.

The *Bouteloua-Stipa* faciation is characteristic of medium-textured soils in the drier part of the brown soil zone, where the climate is unfavourable to mid-grasses; it also occurs in dry situations in the region where the *Stipa-Bouteloua* faciation is predominant. The dominant grasses are *Bouteloua gracilis* and *Stipa comata*, the latter less important than the first. There are three layers, as in the preceding community, but the upper layer is much decreased in importance and the middle layer is decreased in height. Forbs and shrubs are abundant, a conspicuous species is *Artemisia cana* Nutt. Dominant, principal and secondary species include 13 grasses, three sedges, 27 forbs, four shrubs, two half-shrubs and one clubmoss. There are an additional 34 minor species considered characteristic. The number of species is large because of the diversity of soil-types occupied. With overgrazing this community degenerates into a short-grass disclimax.

The *Stipa-Agropyron* faciation is found on undulating soils of medium texture in the dark-brown soil zone, and on relatively level loam soils in the moister part of the brown soil zone. The dominant species are: *Stipa spartea* var. *curtiseta*, *Stipa comata* and *Agropyron dasystachyum* (Hook.) Scribn. These are mid-grasses, and this community is more luxuriant than the two just discussed. Sedges are of relatively greater importance in this community. The total cover of forbs is much as in the *Stipa-Bouteloua* faciation, but *Artemisia*

tridentata is of greater importance. This faciation is not as well investigated as some others.

The *Agropyron-Koeleria* faciation occurs on clay deposits on the beds of former glacial lakes. The soils in these sites have a high water-retaining capacity. Their agricultural value has made undisturbed sites rare. The grasses in this faciation are few in number and are all mid-grasses. The dominants are *Agropyron dasystachyum* and *Koeleria cristata.* Dominant, principal and secondary species include seven grasses, one sedge, and 23 forbs and shrubs; there are also 13 forbs and one shrub of minor importance.

The *Bouteloua-Agropyron* faciation occurs on clay loam solonetzic soils developed on thin boulder clay and modified by preglacial sediments. These soils are droughty because of impermeability and location for the most part in the drier part of the brown soil zone. The principal dominant is *Bouteloua gracilis,* with *Agropyron smithii* Rydb. as a second dominant. The general appearance is that of a short-grass plain, but the mid-grasses play an appreciable role. *Artemisia cana* is less important than in the *Bouteloua-Stipa* community, *Opuntia polyacantha* Haw. and certain other plants are more important than in that community.

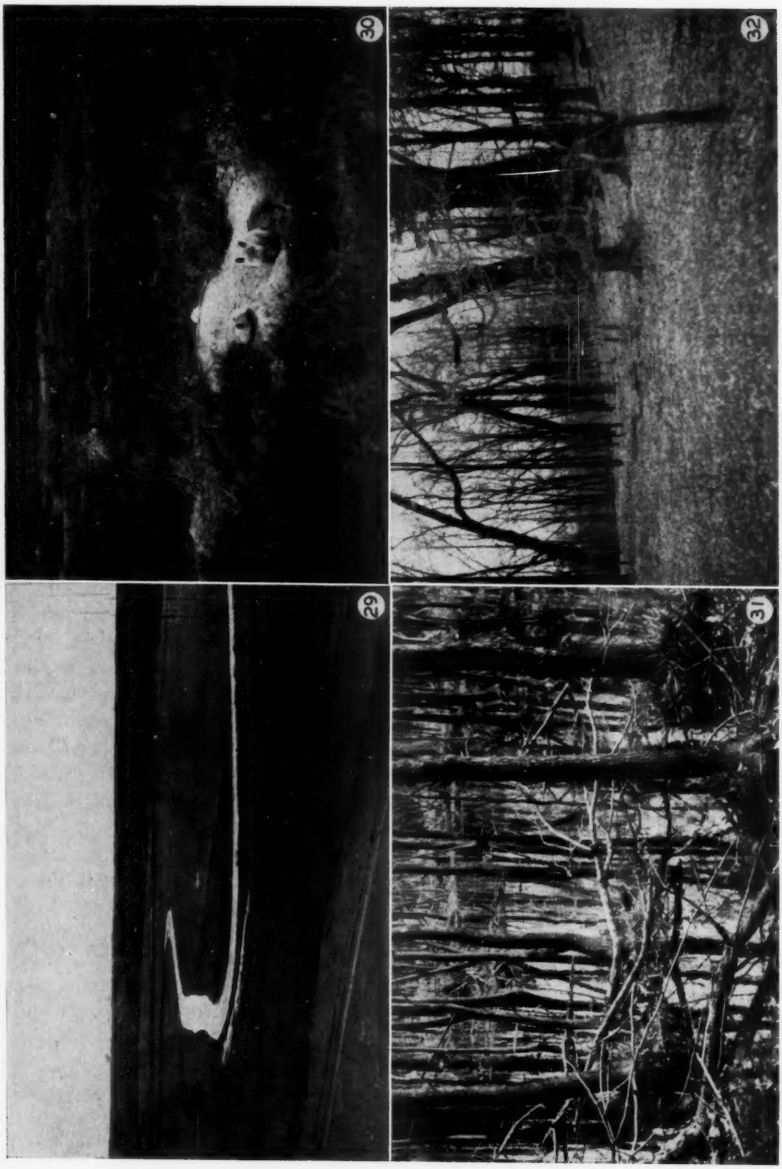
In addition to these climax communities various seral, subclimax and disclimax communities are important in the mixed prairie. The more important natural communities in this group are: (1) in sloughs and coulees, a late hydrosere including tall grasses and coarse sedges, fringed with shrubs, especially *Symphoricarpos occidentalis;* (2) on salt flats, a community characterized by such halophytes as *Distichlis stricta* (Torr.) Rydb., *Puccinellia airoides* (Nutt.) Wats. & Coult., *Salicornia rubra* Nels., *Suaeda* spp., and *Sarcobatus vermiculatus* (Hook.) Torr.; (3) on slightly alkaline clay flats and on some alluviated clay flats, the *Agropyron smithii* consocies, dominated by that species, with *Bouteloua* and *Stipa comata* rare or lacking; (4) the *Agropyron-Muhlenbergia* facies, developed from *Stipa-Bouteloua, Bouteloua-Stipa,* or *Stipa-Agropyron* faciations on water-eroded soils; this is dominated by *Agropyron dasystachyum* and *Muhlenbergia cuspidata* (Torr.) Rydb., with *Bouteloua gracilis* and the two common *Stipa* species reduced in numbers as compared with the climax; (5) on stabilized sand-hills a postclimax tall-grass vegetation composed of such species as *Calamovilfa longifolia* (Hook.) Scribn., *Sporobolus cryptandrus, Oryzopsis hymenoides* (R. & S.) Ricker, and *Elymus canadensis* L.

Communities influenced by man include grazed, cultivated and abandoned lands. The effects of grazing on mixed prairie have been studied by Clarke, Tisdale and Skoglund (1943). The general effect is at first a reduction of mid-grasses, the absolute decline but relative increase of *Bouteloua gracilis* and other short grasses, and the increase of *Poa secunda* and *Artemisia frigida.* With heavier grazing mid-grasses are greatly reduced and short grasses somewhat so, and there is a great increase of unpalatable forbs. Depletion of grass cover and trampling lead to greatly increased erosion; destruction by gophers and insects is more severe on overgrazed grassland.

Abandoned lands show a succession from annual weeds through perennial forbs and short-lived grasses to the climax of rhizomatous native species. Establishment of mature vegetation may take from 15 to 50 years.

True Prairie Region

Weaver and Clements (1938) consider that this region extends into southern Manitoba; according to Coupland (1952) the limited available evidence supports this view, but the region in Canada is little studied and much modified by



Figs. 29-32. Fig. 29, Mixed prairie, Qu'Appelle R., Sask. Science Service. Fig. 30, True prairie near Lytleton, Man., showing family of foxes. Science Service. Fig. 31, Hydric subclimax mixed deciduous forest, southern Ontario. Science Service. Fig. 32, Beech-maple climax forest, somewhat thinned, near Hamilton, Ont. Courtesy J. E. H. Martin.

cultivation. The major dominants are sod-forming and bunch grasses of the mid-grass group. Such species as *Andropogon gerardii* Vitman, *A. scoparius* Michx., *Panicum virgatum* L., *Stipa spartea*, *Sporobolus heterolepis* (Gray) Gray, and *Koeleria cristata* were listed by Bird (1927) as dominants in a community studied by him in Manitoba (Fig. 30). According to Ellis (1938), the grasslands of the Red River Valley are inhabited by "tall" (?mid-) prairie grasses on the better-drained soils, whereas on poorly drained soils these are replaced by grasses of the meadow type. In contrast the prairies of the western part of the Province are of mixed "tall" and short composition. It is likely that a broad ecotone between true and mixed prairie exists here, as described by Weaver and Clements for more southerly regions. Overgrazing in true prairie may lead to formation of a *Poa pratensis* consocies (Coupland 1945). Weaver and Clements state that there are more striking plant societies in the true prairie than in any other grassland region. In the absence of specific information on Canadian situations, however, there seems little value in discussing these.

Fescue Grassland Region

This region has been monographed by Moss and Campbell (1947) for Alberta and by Coupland and Brayshaw (1953) for Saskatchewan. The climate is slightly cooler and more humid than that of the mixed prairie region, which it adjoins. Mean annual temperatures range from 33 to 35°F., mean annual precipitation from about 13.5 to about 16 inches. *Festuca scabrella* is the dominant grass; other important species are *Agropyron subsecundum* (Link) Hitch., *A. trachycaulum* (Link) Malte, *Danthonia intermedia* Vasey, *Helictotrichon hookeri* (Scribn.) Henr., *Koeleria cristata*, and *Muhlenbergia richardsonis* (Trin.) Rydb. There is a fairly wide ecotone with mixed prairie, and in this *Stipa spartea* var. *curteseta* is often a co-dominant. The fescue grassland is the grassland phase of parkland transitions to boreal and montane forests, and extends in gradually diminishing tracts to the northern limit of the aspen grove section in the western half of that ecotone. As might be expected, there are considerable local differences in the composition of the fescue association: in the Cypress Hills Coupland and Brayshaw consider nine grasses, two sedges, 45 forbs, two shrubs and one clubmoss important constituents of the association, whereas in the aspen grove region of Saskatchewan they consider 15 grasses, three sedges, 62 forbs, four shrubs and one clubmoss important. In Alberta the variety of important plants is probably even greater, but accurate comparisons are not available.

Preclimax communities of mixed prairie species occur in exposed habitats, and postclimax communities of aspen, willow, or grasses occur in depressions and on protected slopes. Large depressions often contain *Carex* meadows surrounded by belts of *Populus tremuloides* Michx. and *Salix* spp. In smaller depressions only the shrub phase may be present while in shallower ones only changes in grass cover occur, described in detail by Coupland and Brayshaw.

Overgrazing results first in increase in relative abundance of *Festuca idahoensis* Elmer and *Danthonia parryi* Scribn. The succession on abandoned land has not been studied in this region.

Deciduous Forest Formation

The deciduous forest formation occupies the region of temperate climate and abundant moisture in the eastern part of North America, north of the Gulf Coastal Plain, and south of an ill-defined coniferous-forest boundary, running partly north and partly south of the Great Lakes-St. Lawrence channel. Greater

availability of moisture permits the development of a forest climax; the complexity and slow development of this climax permits more numerous and more varied successions than can exist on the prairies. The whole region is divided conspicuously into a northern glaciated and a southern unglaciated part. The latter (unrepresented in Canada) contains a rich array of species that have survived and developed with only local or altitudinal migrations during the Pleistocene, the former contains a mixture of southern invaders and northern relict forms.

The northern sector of the deciduous forest formation enters the southern part of Eastern Canada in a zone of varying extent. Although the proportion of the total area of Canada occupied by deciduous forest is small, the deciduous forest zone is the longest-settled and most densely populated part of the country, owing to its favourable climate and its east-facing waterways. Partly because of the transitional nature of the more northerly part of the region and partly because of the misconceptions of early workers, the nature of the deciduous forest in Canada has given rise to considerable confusion and controversy. The general classification of Braun (1950) has the advantages of simplicity and of being based on data drawn from the deciduous forest formation as a whole. I have therefore adopted it with more detailed subdivision based on data from Halliday (1937) and Candy (1951).

Braun recognizes three regions as entering Canada: (1) the beech-maple region, occupying the north shore of Lake Erie and the western end of Lake Ontario; (2) the hemlock-white pine-northern hardwoods region, equivalent to the Great Lakes-St. Lawrence region plus the Acadian region of Halliday, occupying a tremendous tract from southeastern Manitoba to the Atlantic coast; and (3) the oak-hickory region, which in modified form enters a short distance into southern Manitoba and southeastern Saskatchewan. The general characteristics of these regions are as follows:—the beech-maple region is characterized by a beech-maple climax, but by an extremely varied moist subclimax forest vegetation, composed in large part of species typical of the more southerly mixed mesophytic forest. More than thirty southern species of trees occur in the Niagara Peninsula that do not occur at Ottawa, and a similar contrast extends throughout the flora and fauna. The hemlock-white pine-northern hardwoods region is more varied. Over much of the eastern part of the region the climax is sugar maple and beech, much as in the beech-maple region, but with an admixture of white pine, *Pinus strobus* L., and hemlock, *Tsuga canadensis* (L.) Carr. In the west beech is absent and sugar maple loses much of its importance: the dominants are pines, which are also subclimax dominants in dry situations farther to the east. In the areas south and east of the St. Lawrence wire birch, *Betula populifolia* Marsh., and red spruce, *Picea rubens* Sarg., are present, the latter as a dominant in some areas. To the north the proportion of boreal vegetation gradually increases, and there is an imperceptible transition to the boreal forest region. Newfoundland is classed by Candy (1951) as part of the Acadian forest region, but both wire birch and red spruce are absent (Macdonald, 1949), and boreal conifers are dominant, though a few species of tolerant hardwoods are present as minority elements. In spite of the presence of many Nova Scotian elements in the fauna and flora it seems advisable to refer Newfoundland to the boreal forest rather than to the deciduous forest formation. The oak-hickory region is represented in Canada by a modified facies from which hickory has already dropped out. This is characterized by Halliday as the oak-aspen section, and is referred by him to the boreal forest, a discrepancy that emphasizes the transitional character of the

Canadian part of this region. The oak-aspen section grades into the aspen parkland to the west and northwest.

Beech-Maple Forest Region

The Canadian part of this region is relatively homogeneous and simple. According to Halliday (1937) and Braun (1950) there is one climax association, consisting primarily of beech, *Fagus grandifolia* Ehrh., and sugar maple, *Acer saccharum* Marsh., together with basswood, *Tilia americana* L., red maple, *Acer rubrum* L., and various oaks, *Quercus alba* L., *Q. macrocarpa* Michx., and *Q. borealis* Michx. f. The characteristic features of this region as compared with the white pine-hemlock-northern hardwoods region are (1) the minor and subordinate status of conifers and (2) the large variety of southerly trees and other organisms that occur in this region and not in the more northerly one (Fig. 31). Hemlock, *Tsuga canadensis*, occurs as scattered individuals within the climax association; white pine, *Pinus strobus*, occurs locally on lighter soils. *Juniperus virginiana* L. is present on poor, gravelly soils. Among trees found here and nowhere else in Canada are: *Juglans nigra* L., *Carya glabra* (Mill.) Sweet, *C. tomentosa* Nutt., *Castanea dentata* (Marsh.) Borkh. (now approaching extinction), *Quercus montana* Willd., *Q. muhlenbergii* Engelm., *Q. velutina* Lam., *Q. coccinea* Muenchh., *Q. palustris* Muenchh., *Morus rubra* L., *Magnolia acuminata* L., *Liriodendron tulipifera* L., *Asimina triloba* (L.) Dunal, *Sassafras albidum* (Nutt.) Nees, *Platanus occidentalis* L., *Cercis canadensis* L., *Gleditsia triacanthos* L., *Gymnocladus dioica* (L.) K. Koch, *Ptelea trifoliata* L. (with an additional isolated station on the St. Lawrence River), *Nyssa sylvatica* Marsh., and *Fraxinus quadrangulata* Michx. A similar representation of southerly species occurs in other plant groups, with the addition of xeric elements such as the prickly-pear cactus, *Opuntia rafinesquii* Engelm. Northern relics appear in the late hydrosere peat bogs, either open with *Chamaedaphne* etc., or more or less closed with larch, *Larix laricina* (DuRoi) K. Koch, black spruce, *Picea mariana* (Mill.) B.S.P., or eastern white cedar, *Thuja occidentalis* L. A more alkaline hydrosere is found in the form of reedy marshes, some of considerable extent. Dry habitats are occupied by pine-oak or oak-hickory communities. This entire region has been tremendously modified by farming and settlement, and areas of undisturbed vegetation are fewer and smaller than in any other part of Canada.

White Pine-Hemlock-Northern Hardwoods Region

This region is one of the most controversial, as well as one of the most varied, in Canada. The modern concept of the region is based on that of Nichols (1935). Halliday (1937) divided the Canadian part of the region into two forest regions, the Great Lakes-St. Lawrence region and the Acadian region. Braun (1950) considered the resemblances more important than the differences and returned to the inclusive concept of Nichols.

The dominants of this region vary widely on both regional and edaphic bases. The principal dominant species are: beech, *Fagus grandifolia;* sugar maple, *Acer saccharum;* hemlock, *Tsuga canadensis;* white pine, *Pinus strobus;* and red spruce, *Picea rubens*. To the north an increasing element of northern conifers — white spruce, *Picea glauca* (Moench) Voss; black spruce, *P. mariana;* and balsam fir, *Abies balsamea* (L.) Mill. — appears, and the characteristic associations of this region give way mosaic-wise to those of the boreal forest.

Throughout the central part of the present region mesophytic sites are characterized by dominance of sugar maple and/or beech (Fig. 32), with the

frequent accompaniment of a variety of other trees, either in the canopy, e.g., *Tilia americana, Betula lutea* Michx. f., *Quercus borealis, Juglans cinerea* L., *Tsuga canadensis* and *Pinus strobus*, or in the understory, e.g., *Ostrya virginiana* (Mill.) K. Koch, *Acer pennsylvanicum* L., and *A. spicatum* Lam. The climax vegetation of this central section has been well characterized by Dansereau (1943). In the part of the region that lies west of Lake Superior red pine, *Pinus resinosa* Ait., and white pine, *P. strobus*, are dominant, and deciduous trees are minor constituents of the vegetation. In the eastern part of the region, in the Maritime Provinces, the deciduous dominants are joined by red spruce, *Picea rubens*, which, though a conifer, resembles white pine and hemlock in that it does not range significantly north of the present region.

Communities in this region are varied. Dansereau (1946) recognizes 30 main communities in the central section, united by complex successional relationships. Four main paths lead to the climax dominated by *Acer saccharum*. The riparian hydrosere leads through *Nuphar* and *Scirpus* stages to successive stages dominated by *Spartina pectinata* Link, by *Calamagrostis canadensis* (Michx.) Nutt., by *Spiraea latifolia* (Ait.) Borkh., by *Populus deltoides* Marsh. and *Salix* spp., by *Acer saccharinum* L. and *Ulmus americana* L., and finally to the climax. The bog hydrosere leads through *Nuphar* and *Carex* stages to stages dominated by *Myrica gale* L., by *Chamaedaphne calyculata* (L.) Moench, by *Ledum groenlandicum* Oeder, *Kalmia angustifolia* L. and *Vaccinium pennsylvanicum* Lam., by *Alnus incana* (L.) Willd., by *Betula papyrifera* Marsh., *Picea mariana*, and *Abies balsamea*, by *Betula lutea* and *Acer saccharum*, and to the climax. This is discussed in greater detail by Dansereau and Segadas-Vianna (1952). The pine xerosere begins on sand with colonization by *Oenothera* spp. and various grasses; this leads to a stage dominated by *Danthonia spicata* (L.) Beauv., which is then invaded in turn by *Festuca rubra* L., by *Agrostis stolonifera* L., by *Poa pratensis* and by *Trifolium repens* L.; then come stages dominated by *Solidago* spp. and other forbs, by *Spiraea* spp. and other shrubs, by *Crataegus* spp. and *Prunus virginiana* L., by *Pinus strobus* (Fig. 33), by *Acer saccharum* and *Tsuga canadensis*, leading to the climax. The birch xerosere may arise on a variety of soils; from the *Solidago* stage this leads through stages dominated by *Betula papyrifera*, by *Acer rubrum*, by *Quercus borealis* and *Tilia americana*, by *Carya ovata* (Mill.) K. Koch and *Acer saccharum*, to the climax dominated by *Acer saccharum* alone. Disclimaxes in this region are very complex; those caused by grazing have been studied by Frankton and Raymond (1944).

Successions essentially similar to those described by Dansereau have been worked out by Gates (1926) in northern Michigan.

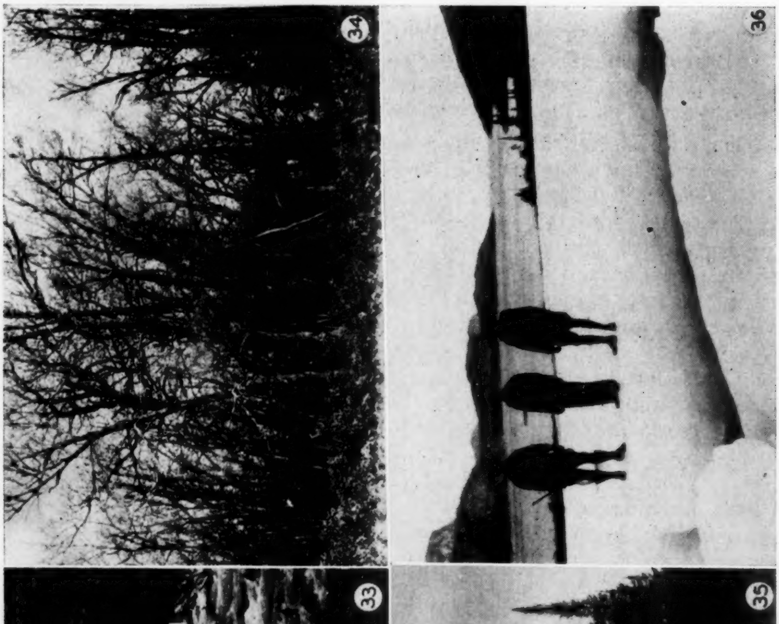
Successions in the western part of the region have hardly been studied. Drexler (1941) in a brief note on the Quetico Provincial Park, considers the climax vegetation to be probably a mosaic of white pine-red pine and white spruce-balsam fir-paper birch communities. Jack pine, *Pinus banksiana* Lamb., forms a seral stage on dry, rocky, clay soil, and a mixed community of uncertain status with black spruce on north-facing slopes. Typical black-spruce bogs form a late stage in the hydrosere. Northern white cedar occurs mainly on lake shores, and is replaced by the spruce-fir-birch community. *Ulmus americana* and *Fraxinus nigra* Marsh. form stands in wet valleys on the sites of old beaver ponds. Scattered specimens of these and other deciduous trees occur elsewhere.

Aside from Halliday's survey of forest sections (1937), there is no general ecological study of the eastern or Acadian part of the region, but Nichols (1918) has contributed a valuable paper on the vegetation of northern Cape Breton

Island. The higher altitudes of Cape Breton belong to the coniferous forest zone, but Nichols considers that the area below 700 feet elevation has in general a deciduous-forest climax. This area, however, differs from those described above in that conifers form a normal and important part of the intermediate successional stages. Other important differences from the central and western parts of the region are: (a) absence of many species that do not range so far to the east, (b) presence of a littoral and halophytic series of communities, and (c) the formation of distinct communities under the influence of exposure on headlands, sea-cliffs and other similar environments.

The climax forest of Cape Breton is dominated by *Fagus grandifolica* and *Acer saccharum*, with an admixture of other deciduous trees, including *Betula lutea, Acer rubrum* and *Betula papyrifera*, and of conifers, including *Abies balsamea, Tsuga canadensis, Pinus strobus* and, in smaller numbers, *Picea* spp. This is usually immediately preceded in the succession by an *Abies-Picea* forest, which on many sites remains as an edaphic climax. Heathy stages in the xerosere also are reminiscent of the coniferous forest zone. Valley and plain xeroseres and fresh-water hydroseres are more normal. Coastal vegetation is of several types. *Rocky sea bluffs* have four zones: an intertidal zone of seaweeds, especially *Fucus* and *Ascophyllum* spp.; a bare zone above high tide, followed by a zone of halophytic crevice plants, e.g., *Plantago juncoides* Lam. var. *decipiens* (Barneoud) Fern. and *Solidago sempervirens* L.; this is followed above the reach of the waves by a zone of shrubs, including *Juniperus horizontalis* Moench, *J. communis* L. var. *depressa* Pursh and *Empetrum nigrum* L. *Sea bluffs of clay or drift* are often almost bare while active erosion is going on, or are populated only by "slump plants", but once stabilized they rapidly develop a rich plant cover. Pioneers are *Equisetum arvense* L., *Agrostis alba* L. var. *maritima* Mey., *Elymus arenarius* L. *sensu lat.* and an assortment of weeds and "slump plants;" these are succeeded by either a grassy sod or a thicket of *Alnus crispa* (Ait.) Pursh var. *mollis* Fern., and these in turn by a forest of *Picea glauca* and *Betula papyrifera;* seepage often leads to the local development of swampy vegetation. *Exposed headlands* are often devoid of forest up to 1,000 ft. elevation; this denudation may be caused partly by human influence, but unsymmetrical trees and the presence of scrubby growth in protected places testify to the effects of exposure. These bare headlands may be clothed either with grasses — *Danthonia spicata, Festuca rubra,* and *Deschampsia flexuosa* (L.) Trin. — or, more often, with low shrubs accompanied by lichens and forbs: *Juniperus* spp., *Vaccinium* spp., *Cladonia* spp., *Polytrichum* spp., *Cornus canadensis* L., *Potentilla tridentata* Ait., *Fragaria virginiana* Duchesne, *Arenaria lateriflora* L., etc.

Beaches may be either stone (shingle) or sandy. *Shingle beaches* have three zones: the lower zone, below high-tide mark, virtually lacks vegetation; the middle or cobble zone has a few conspicuous species that grow as isolated plants — *Cakile edentula* (Bigel.) Hook., *Lathyrus japonicus* Willd. var. *glaber* (Ser.) Fern., and *Mertensia maritima* (L.) S. F. Gray; the upper zone, mostly out of reach of the waves, has the shingle clothed with many species of lichens, and a fairly rich vegetation, including many species of weeds and grasses, a variety of forbs, various xerophytic mosses, *Cladonia* spp. and various trees and shrubs, including junipers and heaths. *Sandy beaches* likewise have an almost plantless lower zone. Their middle zone has the same species as the middle zone of shingle beaches, with others, such as *Ammophila breviligulata* Fern., *Salsola kali* L., and *Arenaria peploides* L.; the upper zone has *A. breviligulata, Lathyrus maritimus* and *Elymus arenarius*. Behind this may be a sandy back-beach area with various



Figs. 33-36. Fig. 33, Blanche R. rapids, near Perkins Mills, P.Q., showing white pine, aspen, and other pre-climax trees. Science Service. Fig. 34, Bur oak forest, Sandilands, Man., showing defoliation by *Anisota* spp. Science Service. Fig. 35, Spruce-balsam forest regenerating, showing admixture of aspen, Algonquin Park, Ont. Science Service. Fig. 36, Subarctic region, at boundary of arctic, Cameron Bay, N.W.T., July, 1937. Science Service.

grasses in an open sward, the sand hidden by *Cladonia* spp. and by such mosses as *Tortula ruralis* (L.) Ehrh. and *Dicranum spurium* Hedw.; there may also be scattered trees, with various plants of protected situations: *Maianthemum canadense* Desf., *Rhus radicans* L., etc.

Salt lakes and ponds contain a restricted vegetation that includes eel grass, *Zostera marina* L., *Ulva* sp. and other algae. *Gravelly shores* have *Plantago juncoides* var. *decipiens*, *Spergularia leiosperma* F. Schmidt, together with various algae and halophytes. The vegetation of *muddy shores* is allied to that of salt marshes, and includes a lower zone of *Eleocharis parvula* (R. & S.) Link, *Triglochin maritima* L., *Ranunculus cymbalaria* Pursh, *Spergularia canadensis* (Pers.) Don. and *Salicornia*, and an upper zone of *Spartina patens* (Ait.) Mühl., *Agrostis alba* var. *maritima*, *Carex mackenziei* Krecz., and *Triglochin maritima*.

Salt marshes are divided into various zones and habitats: the pioneer zone is characterized by *Spartina alterniflora* Loisel.; the salt meadow, submerged only a few hours daily, has *S. patens* as a dominant, with *Distichlis spicata* (L.) Greene, *Triglochin maritima*, *Plantago juncoides* var. *decipiens*, and *Limonium carolinianum* (Walt.) Britt.; the high shoreward reaches are dominated by *Juncus balticus* Willd., the ecological equivalent of *J. gerardi* Loisel. in more southerly marshes; salt pans may be quite barren or may have *Salicornia europaea* L., *Spergularia canadensis*, and a few other species.

Brackish marshes in their wetter parts have a rank growth of *Scirpus* spp. and *Carex* spp. On higher parts *Juncus balticus* var. *littoralis* Engelm. and *Agrostis alba* var. *maritima* are dominant. There are all degrees of transition to fresh-water swamp and bog.

Floristic and phytogeographic information on the maritime part of the region is given in papers by Dore and Roland (1942) and Roland (1946), to which the reader is referred.

Halliday (1937) has given a detailed classification of the forests of the present region, which, as already noted, he divided into two: the Great Lakes-St. Lawrence region with 13 sections and the Acadian region with seven sections. Generalized outlines of his regions, modified to accord with recent information, can be seen on the coloured map (Fig. 26). A more detailed map accompanies Halliday's report, and an edition revised to include Newfoundland accompanies Candy (1950). Halliday's sections correspond to a considerable extent to general biotic divisions. The following list summarizes the sections and their characteristics very briefly. Numbers preceded by L belong to Halliday's Great Lakes-St. Lawrence Section, numbers preceded by A belong to the Acadian Section.

L1, Huron-Ontario Section. This is the sedimentary region of southern Ontario south of the Canadian shield and north of the beech-maple forest region. *Acer saccharum* and *Fagus grandifolia* are the climax dominants; there is an appreciable admixture of southern forms.

L2, Upper St. Lawrence Section. This is the sedimentary region of the lower Ottawa and upper St. Lawrence valleys, centering on Montreal and Ottawa. *Acer saccharum* and *Fagus grandifolia* are the climax dominants; the climate is cooler and the number of southern intrusives is much smaller than in section L1.

L3, Lower St. Lawrence Section. This is the northeastward continuation of L2, from Sorel to the Island of Orleans. The climax is as before, but with beech less important and with an admixture of boreal-forest elements. This

represents the northern limit of such species as *Juglans cinerea* and *Acer saccharinum.*

L4, Algonquin-Laurentides Section. This comprises the Canadian Shield region from Georgian Bay and Lake Temiskaming south of the Ottawa Valley to Brockville, Ont., and north of the Ottawa and St. Lawrence Valleys to La Tuque and Ste. Anne de Beaupré, P.Q. The climax dominant is *Acer saccharum,* but there is considerable admixture and interdigitation of boreal-forest species. *Picea rubens* is present but not important (Heimburger and Porsild, 1938). Shallow-soil and bog areas are much more important than in previous areas because of glacial scouring on resistant rocks and accompanying frequency of undrained hollows. Dansereau's papers, previously cited, apply chiefly to this section. Ray's (1941) site-type analysis of Lake Edward, Champlain Co., shows an instructive example of a mosaic of boreal and hardwood communities towards the northern boundary of the section.

L5, Eastern Townships Section. This occupies the southern part of the Appalachian region in Eastern Townships of Quebec. The general facies is more boreal than in L1 to L3, because of higher elevation. The climax dominant is *Acer saccharum,* replaced by *Picea* and *Abies* at higher altitudes and on thinner soils.

L6, Temiscouata-Restigouche Section. This comprises the south shore of the lower St. Lawrence River from Montmagny to Cap Chat and isolated pockets beyond, the Matapedia and Restigouche valleys, and the western and northern shores of the Bay of Chaleur, on Appalachian sedimentary rocks. The climax dominant is *Acer saccharum; Tsuga canadensis* is absent; boreal-forest species are present in considerable numbers; *Picea rubens* is unimportant. *Thuja occidentalis* is important and characteristic. *Betula papyrifera* and *B. populifolia* are both numerous, especially following fire. Estuarine or fully marine conditions in the St. Lawrence and the Bay of Chaleur are reflected in the presence of numerous halophytes; this section is famous for its relicts and endemics, often of northern or western affinities.

L7, Saguenay Section. This occupies the Lake St. John basin, the Saguenay valley, and the north shore of the St. Lawrence from Tadoussac to Baie Comeau. The flora is essentially similar to that of section L4.

L8, Haileybury Section. This is a small triangular section, centering on Haileybury, Ont., on clay deposits from glacial Lake Barlow. *Picea mariana, Abies balsamea, Populus tremuloides* and *Betula papyrifera* are numerous. Many southern species of trees are present as individuals or communities.

L9, Timagami Section. This lies between Section L10 and the Boreal Forest Region, on sands and gravels derived from glacial Lake Algonquin. *Pinus strobus* is dominant, with *P. resinosa, Picea glauca, Betula papyrifera, Populus grandidentata* Michx., and *Picea mariana* common, and *Betula lutea* and *Acer saccharum* present locally or in small numbers. *Pinus banksiana* is numerous on poor soils and as a fire tree.

L10, Algoma Section. This lies on Precambrian rocks along the north shores of lakes Huron and Superior from Blind River to Michipicoten Harbour, Ont. Climax dominants on ridge-tops are *Acer saccharum* and *Betula lutea. Pinus strobus* and *Thuja occidentalis* are dominant on southward-facing slopes. *Picea glauca* is widely developed along river flats.

L11, Quetico Section. This includes the glaciated, thin-soiled Canadian shield territory along most of the length of the Rainy River. The climax

dominants are *Pinus strobus* and *P. resinosa;* much of the area is occupied by fire-communities of *Pinus banksiana, Abies balsamea, Picea glauca* and *P. mariana, Betula papyrifera* and *Populus grandidentata.* Such hardwoods as *Betula lutea, Ulmus americana, Acer saccharum* and *A. negundo* L. form communities along river banks and occur as scattered individuals elsewhere. *Ostrya virginiana* (Mill.) K. Koch is of general distribution.

L12, Rainy River Section. This extends along the upper Rainy River, on flat, poorly drained plains and low uplands, on lacustrine and morainic deposits. *Pinus strobus* and *P. resinosa* are perhaps dominant on upland sites, but are now to a considerable extent removed by human influence and by fire, and replaced by *Populus balsamifera* L., *Pinus banksiana,* and perhaps an increased proportion of *Picea glauca.* Tolerant hardwoods occur along the river banks and as scattered individuals elsewhere. The extensive swampy sites are occupied by *Picea mariana, Larix laricina, Thuja occidentalis* and by *Salix* and *Alnus* scrub.

L13, Lake Superior West Section. This lies on Precambrian sedimentary rocks covered by clays and sands deposited by glacial Lake Algonquin, west of Lake Superior adjacent to the Minnesota border. It is occupied by mixed forest with *Pinus strobus, Acer saccharum, Picea glauca, Betula lutea* and *Tilia americana* on higher land, *Acer rubrum* and *Thuja occidentalis* on wetter sites. Burned areas have *Populus grandidentata, Betula papyrifera, Picea glauca, Abies balsamea* and some *Pinus strobus.*

A1, New Brunswick Uplands Section. This is an area of granitic intrusives and folded Appalachian sedimentaries in the northwestern part of the province reaching elevations up to 2,700 ft. The forest is mainly coniferous, with *Abies balsamea* predominant, *Picea mariana* associations common, especially on stony slopes, and *P. rubens* generally distributed, occurring on more favourable sites mixed with *Pinus strobus, Thuja occidentalis, Acer saccharum, Betula lutea, B. populifolia* and *Tsuga canadensis.* Fire trees are *Betula papyrifera, B. populifolia* and *Pinus banksiana.*

A2, Miramichi Section. This is in the north central area of New Brunswick on gently undulating plains underlain mainly by sandstones, conglomerates and shales, covered by light, sandy soils deficient in lime. The forest cover is mixed or coniferous; much of it is secondary following destructive fires in the 19th century. *Tsuga canadensis* was probably much more important formerly than now. *Pinus* spp. have been reduced by lumbering. Hardwoods are more important on better soils, especially on high ground and in the west.

A3, Northeast Coastal Section. This comprises the coastal portion of the plain occupied by section A2, and has similar soils. Conifers are predominant; trees are often dwarfed near the coast, where there are large poorly drained areas of swamp, bog and barrens. *Picea mariana* is dominant, accompanied by *Thuja occidentalis, Larix laricina, Betula papyrifera* and *B. populifolia; Picea rubens* is well distributed; *Pinus banksiana* occurs extensively on sand flats. Hardwoods are restricted to small areas on ridges.

A4, Central Section. This occupies southern and western New Brunswick, Prince Edward Island and western Nova Scotia. It is a varied section comprising all the more southerly elements of the region. The forest is generally deciduous, with *Acer saccharum, Fagus grandifolia* and *Betula lutea,* accompanied by *Picea rubens, Pinus strobus* and *Tsuga canadensis.*

A5, Atlantic Slope Section. This occupies the entire Atlantic Coast of Nova Scotia. Trees include *Picea rubens,* often mixed with *Acer saccharum,* etc. The growth is often somewhat reduced, bogs and barrens are prevalent.

A6, Cape Breton Plateau Section. This is considered by Nichols to have a coniferous climatic climax, and is therefore logically classifiable with the boreal forest region. *Abies balsamea* is dominant, with *Picea glauca* and *P. rubens* also important. Exposed areas are occupied by heathy barrens with *Cladonia* spp. and spruce krummholz. These lack arctic and subarctic species and are mainly the result of exposure and scanty soils.

A7, Cape Breton Plains Section. This has already been described in the general account of the region.

Oak-Hickory Region

As previously indicated, this region is represented in Canada by the transitional oak-aspen section, which can equally well be referred, as was done by Halliday, to the aspen grove division of the boreal forest region. The presence of many southern species and a general similarity to the typical oak-hickory areas to the south makes Braun's assignment of it attractive, and it is followed here. Although Halliday maps it as a solid area, Shantz and Zon's (1924) representation of narrow tongues of woodland extending along river valleys is probably more accurate. *Populus tremuloides* is the most prevalent species, but *Quercus macrocarpa* Michx. is characteristic, recurring as scattered individuals away from rivers and in some numbers on flood plains. *Ulmus americana, Tilia americana, Fraxinus* spp. and *Populus* spp. occur on alluvial soils along rivers.

Bird (1927) gives an account of deciduous forest vegetation in the Treesbank-Aweme area, Man. (Fig. 34). Primary undergrowth species include *Juniperus horizontalis, Amelanchier spicata* K. Koch., *Prunus virginiana* L., *P. pensylvanica* L. f., *Salix bebbiana* Sarg., *S. discolor* Muhl., *Symphoricarpos albus* (L.) Blake, *Rosa blanda* Ait., *R. acicularis* Lindl., *Rhus radicans, Arctostaphylos uva-ursi* (L.) Spreng., *Corylus americana* Walt., and *Heliopsis helianthoides* (L.) Sweet var. *scabra* (Dunal) Fern. Bird describes various other habitats in this region.

Coniferous Forest Formation

The coniferous forest formation comprises a variety of forest types that are only in part climatically equivalent. There are two primary divisions: the northern forests and the Cordilleran forests. The former are here divided into a boreal region of closed forest and a subarctic region of open forest. The subalpine zone of the Cordilleran region is the representative there of the boreal and subarctic regions. The lower Cordilleran zones have more temperate climates, but agree with the northern and subalpine forests in having conifers as climax dominants. All the coniferous forests contain important quantities of broad-leaved trees but these are restricted to a few species of the genera *Betula* and *Populus* in the north, with the addition of *Alnus* and *Acer* in the west. These deciduous components are almost always restricted to preclimax seral stages: only in the xeric areas on the border of the formation do they become dominant in the climax.

Boreal Forest Region

The boreal forest region is one of the most widespread and characteristic of Canadian environments, and is the geographic representative of the taiga zone of Europe and Asia. Halliday recognizes a major division into a moister eastern part and a drier western part, but on the whole this zone is one of the most uniform vegetational areas of comparable size in the world. In the interior plains the large expanse of coniferous forest is flanked on the south by a transition zone to the grassland formation. This is the aspen grove section of

Halliday, which is here treated as part of the boreal forest region, though the fescue grassland penetrates mosaic-wise far into it. An additional transition zone lies to the north, between the boreal forest and the tundra. This is treated by Halliday as part of the boreal forest region, but from the entomological standpoint it has enough peculiarities to justify its separation as a distinct subarctic region. Recent writers on the vegetation of Labrador and New Quebec go so far as to divide the subarctic region as here conceived into two regions (Hustich, 1949; Rousseau, 1952), but for our purpose this is an unnecessary refinement. Halliday did not discuss the forests of the island of Newfoundland. These have been described by Robertson (1945) and by Candy (1951); the latter author assigns them tentatively to the Acadian forest region, mainly on the basis of resemblance to the forests of Cape Breton Island. However, most of the forested region is dominated by *Picea glauca*, *P. mariana*, and/or *Abies balsamea*. Moreover, site-type studies indicate that only about five per cent of forests in Newfoundland belong to types in which white pine and tolerant hardwoods play an important part; all forests occupy less than half the area of the island. *Betula populifolia* and *Picea rubens*, the two characteristic trees of the Acadian forest region are absent from Newfoundland, and most of the characteristic trees of the hemlock-white pine-northern hardwoods region as a whole are either absent from the island or of very restricted distribution in it. In view of these facts it seems more realistic to include Newfoundland in the boreal forest region.

Weaver and Clements (1938) describe the typical association of the boreal forest. The climax dominants are *Picea glauca* and *Abies balsamea*. *Larix laricina* and *Picea mariana* occur on wet sites, and the latter forms an edaphic climax on rocky plateaux and high mountain slopes. *Pinus banksiana* is characteristic of sandy and other dry habitats. The undergrowth typically consists of such plants as *Gaultheria procumbens* L., *Vaccinium oxycoccus* L., *Cornus canadensis* L., *Mitchella repens* L., *Epigaea repens* L., *Coptis groenlandica* (Oeder) Fern., *Clintonia borealis* (Ait.) Raf., *Pyrola elliptica* Nutt., *Gaultheria hispidula* (L.) Bigel., *Aralia nudicaulis* L. and various mosses and lichens.

Bog successions are essentially similar to those of the white pine-hemlock-northern hardwoods region except in their terminal stages, which of course lead to a different climax. Detailed accounts are given for the eastern part of the region by Dansereau and Segadas-Vianna (1952) and for the western part by Lewis and Dowding (1926), Lewis *et al* (1928 and Moss (1953). Fire successions vary somewhat. In the eastern division the most typical fire succession leads through an herbaceous stage in which *Epilobium angustifolium* L. and *Pteridium aquilinum* (L.) Kuhn var. *latiusculum* (Deso.) Underw. are prominent, through a *Populus tremuloides-P. grandidentata-Betula papyrifera* community to re-establishment of the climax (Fig. 35). In northwestern fire successions *Pinus banksiana* is relatively more important and *Populus balsamifera* is an important constituent, according to Raup (1946).

Exclusive of areas here referred to other forest regions, Halliday divides the boreal forest region into 24 sections, determined partly by climate, but very largely by edaphic factors. To these may be added the two sections recognized by Candy in Newfoundland. In the main the sections differ in proportions of widespread vegetation-types rather than in well-marked characteristics of species-composition. The region is so uniform and our knowledge of the distribution of its insect fauna is so scanty that there seems little value in listing the sections in detail. Certain general tendencies may, however, be noticed.

The main overall climatic tendencies are a precipitation gradient declining to the west and a temperature gradient declining to the north. The northward-declining precipitation gradient is counteracted by decreasing evaporation, so that the precipitation-effectiveness actually rises towards the north, at least in the western part of the region. Following the precipitation gradient there is a tendency for humid vegetation-types to predominate in the east; on the poorly drained lands of the Canadian shield there is a tremendous development of bogs and muskegs, and black spruce and larch habitats are predominant in many of Halliday's eastern sections. In the west the dry jack-pine habitats are much more widespread, and transitions to grassland and parkland are common far north of the main grassland region (Dawson, 1888; Raup, 1934, 1935, 1945). In the west, too, *Populus balsamifera* plays a more important part in successions. The north-south gradients also make themselves felt. In the east there is an infiltration of southern elements, notably white pine and the tolerant hardwoods, into a number of more southerly areas: Newfoundland, north-central Ontario, etc. In the west the true coniferous forest gradually gives way southward to poplar associations and the aspen parkland. To the north the richness of the flora diminishes (Hustich, 1949; Raup, 1946) and the transition to open subarctic conditions is gradual.

Aside from these ecologically determined differences there are others of historic-geographic origin. In the west there are strong infiltrations of Cordilleran and Alaskan species and forms: *Pinus contorta* Dougl. var. *latifolia* Engelm., *Betula papyrifera* Marsh var. *neoalaskana* (Sarg.) Raup, and *Picea glauca* (Moench) Voss var. *albertiana* (S. Brown) Sarg., together with many non-arboreal species. In the east, too, there are characteristic plants of various geographic origins: eastern species of wide distribution, such as *Thuja occidentalis*, coastal plain plants that remain as relicts of the Champlain Sea (Dutilly and Lepage, 1945; Fernald, 1932; Marie-Victorin, 1938; Potter, 1932), and various Gulf of St. Lawrence relicts or radiants (Fernald, 1924, 1925; Marie-Victorin, 1938; Scoggan, 1950).

Among useful regional studies of the boreal coniferous forest are those of Robertson (1945) dealing with Newfoundland, Nichols (1918) on Cape Breton Island, Harrison (1934) and Halliday (1935) on Manitoba, Moss (1932, 1953) on Alberta, and Raup (1934, 1935, 1946) on the Northwest. Some of these areas present a few special features. In Cape Breton Island and Newfoundland extensive areas of heath-lichen barrens occur. The barrens of Cape Breton are believed by Nichols to be edaphically rather than climatically controlled; they are composed essentially of an attenuated boreal xerophytic flora, and lack characteristic arctic and subarctic species. The barrens of Newfoundland have not been thoroughly studied.

In the northwest a number of forest communities have been distinguished by Raup (1946) in the Athabaska-Great Slave Lake area and by Moss (1953) in northwestern Alberta. The two areas share several communities, but each has some not found in the other. In the Great Slave-Athabaska area a considerable proportion of the woodland is of the open lichen-forest type, and is referable to the following region. In favourable upland sites on sedimentary rocks a typical white-spruce forest with mossy floor characterized by *Salix bebbiana* and *Hypnum* spp. is widespread. On flood-plains, deltas and other very young surfaces a shrubby white spruce forest, with *Viburnum edule* (Michx.) Raf. and *Cornus stolonifera* Michx., in addition to *Picea glauca* and *Salix bebbiana*, arises from a succession of several species of shrub willows

followed by *Populus balsamifera;* all stages of *Salix-Populus* and *Populus-Picea* transitional communities are found. On the Canadian shield and on sandy soils elsewhere forests dominated by *Pinus banksiana* are common. Invariably associated species are *Betula papyrifera* var. *neoalaskana, Arctostaphylos uva-ursi, Cladonia rangiferina* (L.) Web. and *Cetraria nivalis* (L.) Ach. There are two subtypes: on rocky terrain additional important species are *Picea glauca, Amelanchier florida* Lindl., *Artemisia frigida* Willd. and *Saxifraga tricuspidata* Rottb.; on sandy soils characteristic species are *Picea mariana, Alnus crispa* (Ait.) Pursh, and *Vaccinium* spp. Along stream valleys a fifth forest type occurs, composed primarily of *Abies balsamea* and *Picea glauca,* with *Betula papyrifera* var. *neoalaskana*, a shrub layer of *Alnus, Cornus* and *Viburnum*, and a thick mat of woodland mosses. On the Caribou Mountain Plateau north of the lower Peace River exists a *Picea mariana-Pinus contorta* forest with a deep moss carpet and the usual coniferous-forest herbs. Finally, bog forests of the usual types are present.

In northwestern Alberta extensive subarctic forests are lacking; in the boreal region most of the forest types just described are present, with the addition of several xeric communities, notably a white spruce-grass-shrub faciation with *Elymus innovatus* Beal, *Shepherdia canadensis* (L.) Nutt., and *Alnus crispa;* a *Pinus contorta*-heath consociation; and a poplar association.

This poplar association and the related aspen parkland together form a major division of the boreal forest region, occupying a zone surrounding the prairie grassland regions and marking a transition to them. The forests and groves of the poplar association are dominated by *Populus balsamifera* and *P. tremuloides,* singly or in combination. Moss (1932) has published a detailed survey of the composition of this association in Alberta. He notes differences between *P. balsamifera* and *P. tremuloides* consociations, and considers the following plants characteristic of the former: *Cornus stolonifera, Salix* spp., *Ribes* spp., *Alnus incana, Picea glauca, Lonicera involucrata* (Richards.) Banks, *Mertensia pilosa* (Cham.) DC., *Equisetum* spp., *Petasites palmata* (Ait.) Gray, *Galium triflorum* Michx., *Mitella nuda* L., *Actaea* spp. and several mosses. Characteristic of the *P. tremuloides* consociation are: *Symphoricarpos albus* (L.) Blake, *Amelanchier alnifolia* Nutt. *Corylus cornuta* Marsh., *Prunus* spp., *Aralia nudicaulis, Cornus canadensis, Maianthemum canadense* Desf., *Schizachne purpurascens* (Torr.) Swallen. In Manitoba, Bird (1930) found *Cornus stonolifera* a subdominant in the mature *P. tremuloides* forest, along with *Corylus americana, Aralia nudicaulis, Pyrola asarifolia* Michx., and *Cornus canadensis.*

In general, in spite of the very distinctive facies of the poplar association, it shows little difference in species composition from the adjacent zone of typical coniferous forests, some of whose seral stages parallel the poplar association closely. The aspen parkland of course includes prairie elements as well as woodland ones, but it has few if any endemic components.

Subarctic Region

North of the zone of continuous coniferous forests lies a belt, sometimes extensive, of more or less open coniferous forest or parkland interspersed with lichen heath or other tundra-like communities (Fig. 36). This zone, essentially the Hudsonian of Merriam, is classed by Halliday as the northern transition belt of his boreal forest region, and, in accord with his division of the region into eastern and western portions he recognizes a northeastern transition section and a northwestern transition section. Hustich (1949) and Rousseau (1952) both recognize the subarctic as an independent zone. Hustich recognizes ten main

forest types, in three series. The *dry series* includes: (1) conifer-lichen forest, with *Picea glauca*, *P. mariana* or, rarely, *Larix laricina* or *Pinus banksiana* on a lichen cover of *Cladonia alpestris* (L.) Rabenh. with an admixture of *C. sylvatica* (L.) Hoffm. var. *sylvestris* (Oed.) Vainio and *C. rangiferina;* (2) conifer-dwarf shrub-lichen forest, like the preceding but with *Betula glandulosa* Michx., *Empetrum hermaphroditum* (Lge.) Hagerup, *Vaccinium* spp., and *Calliergonella* sp. (Willd., Br. & Sch.) Grant and other feather-mosses, together with *Dicranum* spp.; (3) conifer-*Vaccinium* forest, with *Picea mariana* and *Vaccinium pennsylvanicum* and sometimes *V. myrtilloides* Michx. and *Kalmia augustifolia* on a feather-moss mat consisting mainly of *Hylocomium splendens* (Hedw.) Big. Eur. and *Pleurozium schreberi.* The moist series includes: (4) the conifer-feather moss forest, with dense ground cover of *Hylocomium splendens, Pleurozium schreberi,* and *Hypnum crista castrensis* (L.) Hedw.; (5) the conifer-bunchberry forest, with reduced moss cover and abundance of *Cornus canadensis, Linnaea borealis* L. and *Trientalis borealis* Raf.; (6) the rich conifer forest, a composite and mainly a boreal type, but occurring in the subarctic region in river valleys, etc.; and (7) the mixed groves, a miscellaneous group. The *wet series* includes: (8) the open bog forest, an acid bog with *Rubus chamaemorus* L., etc. and scattered old trees of *Picea mariana* and *Larix laricina;* (9) the black spruce muskeg, with *Sphagnum* spp. and bog shrubs; and (10) the rich swamp forest with *Picea glauca* and *Larix laricina* and reduced abundance of *Sphagnum* spp. Hustich (1951), Wenner (1947), and Rousseau give more detailed notes on certain communities.

Raup (1946) recognized five variants of the "park-like white spruce forest" in the Great Slave Lake region: (1) on sand plains, *Picea glauca, Betula papyrifera* var. *neoalaskana, Cladonia rangiferina, C. alpestris* and *Cetraria islandica* (L.) Ach., with various shrubs and forbs; (2) on sandy ridges, a partly bare surface, with ground vegetation including *Empetrum nigrum* and the lichen *Stereocaulon paschale* (L.) Hoffm.; (3) on stony plains and beach ridges, *Picea glauca* in nearly pure stands, with *Cladonia* spp., *Cetraria* sp. and a mat of *Dryas* spp.; (4) in the higher shore zone, a denser flora like (1) but with some added secondary species; (5) on higher stony ridges, a more mesophytic ground cover, with a thick carpet of woodland mosses, various heaths, etc.

In addition to the parkland and fragmentary forests that characterize the region, there are of course additional widespread vegetation types: a bog succession similar to that farther south, but poorer in species; willow-birch thickets along stream beds, *Carex* meadows, etc.

On the south the subarctic region intergrades to the boreal forest region. In much of eastern Canada a rather sharp boundary is formed by the mountain ranges lying north of the St. Lawrence River and Gulf of St. Lawrence. Farther west the boundary is less precise, and in the Northwest Territories there are long interdigitations of the two regions. In the basin of the lower Hamilton River and farther north along the Koksoak River, the great sedimentary belt of the Labrador-Quebec peninsula supports a vegetation that is probably best considered an isolated representative of the boreal forest. On the north the limits of the subarctic zone are probably mainly climatic (Villeneuve, 1946). This seems to be the case in the interior of Labrador and Quebec (Hustich, 1949), at Churchill, Man., and in the Northwest Territories (Clarke, 1940). On the east coast of Hudson Bay, Marr (1948) considers the limit to be edaphic, in contrast to the regions previously mentioned. Here there is no sign of dwarfing of trees on favourable soils, even under conditions of exposure.

However, young, scraped rock-surfaces predominate in the region he studied, and there has apparently not been time since deglaciation for suitable mineral soils to develop by weathering. Raup considers that climate, soil-type and soil-history are all three important in the Great Slave-Athabaska region, and this will probably turn out to be the soundest view for the majority of subarctic environments.

Although the general similarity of the eastern and western parts of the subarctic region is apparent, there are important differences in subsidiary elements of the biota, and the eastern and western subdivisions of Halliday appear justified. Whether the best boundary line is at the obvious geographic barrier of Hudson Bay or a little farther to the west, where the boundary of many species ranges seem to lie, remains to be decided by future investigations.

Hustich (1949) and Rousseau (1952) have given classifications of the eastern section of the subarctic region; both recognize a division between a southern zone of essentially continuous bog and open forest (*taiga* of Hustich, *subarctic* of Rousseau) and a northern zone of tundra with subarctic forest extending along valleys and other protected places (*forest-tundra* of Hustich, *hemiarctic* of Rousseau). The differences between these are mainly of relative area occupied by constituent associations rather than in the associations themselves, and although from a life-form and forestry point of view the dissimilarities are important, from the biogeographic standpoint they are less so. In his "taiga" area Hustich distinguishes a western section with *Pinus banksiana*, and an eastern section in which this tree is lacking; his forest-tundra area he leaves undivided. Hustich divides the Hamilton River-Koksoak River sedimentary zone into two along the height of land. Although there is throughout a contrast between the flora of the sedimentary zone and that of the igneous region on each side of it, Halliday's arrangement, which shows the lower portion of the inland parts of the two basins as boreal and the higher region around the height of land as subarctic, is perhaps more realistic.

Interrelations of Cordilleran Forest Regions

For most of its length the North American Cordillera runs north and south, usually in a series of rather well-defined ridges and valleys with relief of the order of 10,000 feet or more. Four main factors influence habitats systematically: elevation, latitude, distance from the sea and precipitation. To these are added the extremely variable local factors of insolation, exposure, drainage, snow cover, soil type and geological substratum. Variations of the latter group make for haphazard local arrangement of communities; regularities of the former group make for a definite overall zoning pattern with on the one hand continuities over distances of thousands of miles along the mountain chain, and on the other hand sharp zonal differences, sometimes in a repetitive pattern over very short distances, across it.

As is well known, altitude and latitude have parallel effects on temperature. Temperature-controlled zones therefore tend to slope downward towards the north: warmer zones tend to "run into the ground" northward, and cooler zones are eliminated by the insufficient height of peaks southward. Daubenmire (1943) shows that this progression is not a linear one, but that timber-line, for instance, descends more sharply in higher latitudes than in lower ones. Precipitation is governed by moisture-laden winds from the Pacific. In general these give rise to wet zones on the western slopes of mountains, the precipitation decreasing with distance away from the coast and with the number of intervening ranges. Major river gaps permit storms and moisture-laden winds to penetrate

into the interior, making inland mountain ranges wetter opposite these points than elsewhere in their course. Coastal species and associations penetrate inward along the storm track that parallels the lower Fraser valley and spread out along the windward slopes of the interior ranges, as shown graphically by Daubenmire (1943:378, Fig. 4). Distance from the sea has an effect on temperatures only partly correlated with its effect on precipitation. This is the well-known difference between maritime and continental climates. Proceeding from the coast inward, the following are differences in Fahrenheit degrees between highest and lowest temperatures ever recorded (Mackie, 1954): Clayoquot, 83; Nanaimo Airport, 94; New Westminster, 101; Hope, 112; Penticton, 121; Vernon, 135; Revelstoke, 135; Fernie, 137. The coastal region is characterized not only by high precipitation and small annual temperature variation, but also by depression of the snow-line, and consequent compression or elimination of upper vegetational zones.

There is substantial agreement on the classification of the Cordilleran forest zones (Halliday, 1937; Weaver and Clements, 1938; Daubenmire, 1943; Spilsbury and Tisdale, 1944). Munro and Cowan (1947) have evolved a somewhat different classification of "biotic areas" based on distribution of vertebrates as well as on general features on the environment; this can be harmonized with the generally accepted zonal scheme with little adjustment. The classification followed here is essentially that of Halliday; the major differences of other classifications are noted under the appropriate regions. Recent studies indicate that the boreal forest region should extend southward along the east face of the Rocky Mountains to a degree not shown in the Halliday map reproduced here. Clarke and Cowan (1945) recognize a definite zone of northern coniferous forest below the subalpine forest at Banff, the replacement of *Picea engelmanni* (Parry) Engelm. by *P. glauca* being taken as the criterion. Lynch (1956) states that true aspen parkland extends along the Rocky Mountains to the United States border and well into Montana. Daubenmire (1956) has published on climatic determinants of vegetation zones just south of the international boundary; his results are presumably applicable to southern British Columbia. He finds that the determinants of zonal boundaries are neither obvious nor uniform. The most popular comprehensive schemes of climatic classification, those of Köppen (1936), of Thornthwaite (1931) and of Thornthwaite (1948) completely fail to explain observed zonal distributions. Daubenmire finds that the lower limit of the subalpine forest is the lowest ecotone to be determined principally by temperature. All lower ecotones are determined primarily by moisture, with temperature as a secondary or negligible factor.

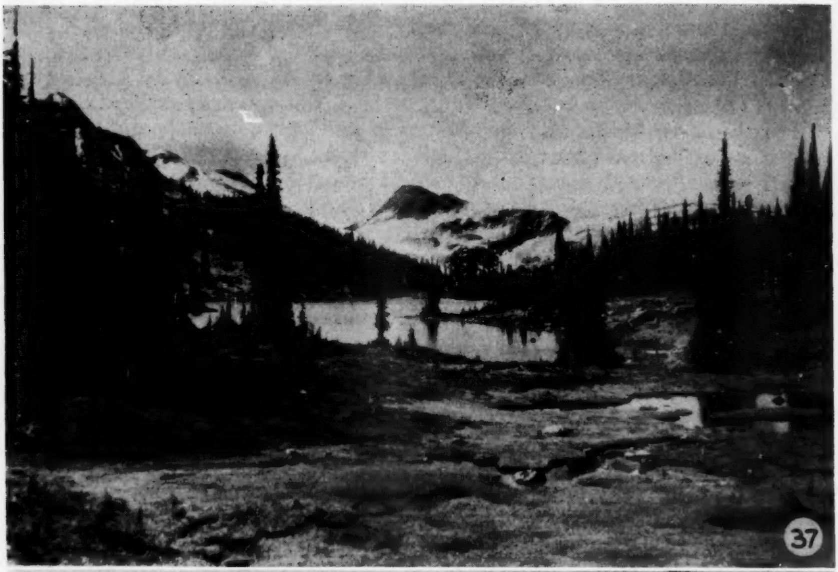
Subalpine Forest Region

This is the Cordilleran equivalent of the boreal forest region; its climax dominants belong to the same genera but to different species, *Picea engelmanni* largely replacing *P. glauca*, and *Abies lasiocarpa* (Hook.) Nutt. replacing *A. balsamea*. The flora consists of three major elements: species shared with the boreal forest region, species shared with the lower Cordilleran zones, and endemic species; the last are partly representatives of boreal species, and partly apparent segregates of species of the lower zones. This region is divisible in all three dimensions. There is a boundary at about the middle of British Columbia between the northern and far northern divisions of Daubenmire, the latter division being characterized by the presence of *Picea mariana* and by some differences in the array of understory plants. A second division is altitudinal:

the upper subalpine zone, with park-like vegetation (Fig. 37) degenerating into krummholz, is distinct in appearance from the lower zone of continuous forest and contains some trees exclusively or in greater abundance, e.g., *Pinus albicaulis* Engelm., *Pinus flexilis* James, and *Larix lyallii* Parl. Spilsbury and Tisdale consider this a distinct zone, but other authors group it with the lower subalpine, which shares the same dominants. The third dimension of division is longitudinal, depending on mountain ranges and exposures. This presents more difficulties, due partly to the complexity of the terrain and partly to lack of field work, and no general classification has been worked out. However, some tendencies are obvious. *Pinus flexilis* and *Larix lyallii* are confined to the easternmost or Rocky Mountain region; towards the west coast *Tsuga heterophylla* (Raf.) Sarg. becomes an important element in the forest, *Tsuga mertensiana* (Bong.) Sarg. is represented, and there are intrusions of *Thuja plicata* Donn and *Abies amabilis* (Dougl.) Forbes.

Along the Rocky Mountains the belt of subalpine forest is essentially continuous; along the Coast Range it is broken, and in the interior it is very much fragmented, to a degree hardly suggested in the generalized map given here. The subalpine forest reaches its northern limit in northern British Columbia, though *Pinus contorta* and *Abies lasiocarpa* extend a considerable distance farther north into the western sections of the boreal forest region (Macdonald, 1949; Porsild, 1951). The southern extension of the zone has been studied by Daubenmire (1953), who finds that it reaches well into Mexico, and who recognizes four latitudinal divisions, of which the two northernmost, as already mentioned, are represented in Canada. The far northern division is limited to Canada; the northern division extends as far south as central Wyoming. The unity of the region lies mainly in its forest cover; there is much less resemblance in the understory florules of the different divisions. In the wet Pacific Coast region, e.g., on Vancouver Island, the subalpine forest is not represented at all, and the coast forest is replaced directly by alplands, with the transitional parkland containing only coast-forest species of trees (Carl, 1943).

Halliday recognizes only two sections: the east slope Rockies section and the interior subalpine section. Daubenmire's work would suggest the division of the former into far northern and northern sections; Halliday himself suggests that his interior subalpine section will probably need division, but data are insufficient for the purpose at present. Daubenmire gives the following undergrowth plants as characteristic of the northern Rocky Mountain section: *Menziesia ferruginea* Hook., *Vaccinium membranaceum* Dougl., *Shepherdia canadensis* (L.) Nutt. and *Xerophyllum tenax* (Pursh) Nutt. He considers the following characteristic of the far northern Rocky Mountain section: *Alnus crispa* (Ait.) Pursh, *Viburnum pauciflorum* Pyl., *Amelanchier florida* Lindl. and *Shepherdia canadensis* (shared with the northern section). Clarke and Cowan (1945) give brief notes on the distribution of the subalpine forest in the Banff area, but do not discuss the local flora. In the Kootenay National Park, on the west slope of the Rockies in southern British Columbia, Munro and Cowan (1944) describe a wet facies of the subalpine forest as having a deeply moss-covered floor, with such plants as *Calypso bulbosa* (L.) Oakes, *Cypripedium calceolus* L. var. *pubescens* (Willd.) Correll, *Orchis rotundifolia* Banks, *Pinguicula vulgaris* L., *Primula maccalliana* Wieg., and *Ledum groenlandicum*. Drier places are covered with a shrubbery including such species as *Vaccinium ovalifolium* Sm., *Rhododendron albiflorum* Hook., and *Menziesia ferruginea*. Carl and Hardy (1945) describe an upper community of the subalpine forest on the east side of the Purcell Range as having *Abies lasiocarpa*, *Larix lyallii*,



Figs. 37-38. Upper subalpine forest, Monashee Mts., B.C. Courtesy of J. D. Gregson. Fig. 38, Lower montane forest, with ponderosa pine. Aspen Grove, B.C. Science Service.

and *Pinus albicaulis* as dominants, with such undergrowth species as *Vaccinium scoparium* Leiberg, *Phyllodoce glanduliflora* (Hook.) Cov., *Leptarrhena amplexifolia* (Sternb.) Ser., *Fragaria bracteata* Heller, *Arnica cordifolia* Hook., *A. latifolia* Bong., and *Aster foliaceus* Lindl. var. *apricus* Gray. *Rhododendron albifolia, Vaccinium membranaceum, Stenanthium occidentalis* Gray and *Silene douglasii* Hook. reach their upper limits here. Munro (1945) notes the subalpine forest in Glacier Park, in the Selkirk Range, as having *Abies lasiocarpa* dominant in the lower zone; in the parkland zone *A. lasiocarpa, Picea engelmanni, Tsuga mertensiana* and *Pinus albicaulis* all occur. There is little underbrush; heathers of the genera *Cassiope* and *Phyllodoce* and *Luetkea pectinata* (Pursh) Hook. are represented. In the Tranquille Range near Kamloops, Spilsbury and Tisdale find the forest ("subalpine") and parkland ("upper subalpine") zones rather sharply distinguished. There is a considerable proportion of *Pinus contorta* in the forest zone. The principal shrubs are *Vaccinium membranaceum, Pachystima myrsinites* (Pursh) Raf., and *Lonicera involucrata* (Richards.) Banks. The herbaceous cover is sparse and is dominated by *Vaccinium scoparium*, but includes a number of other species, many of them shared with the boreal forest region: *Cornus canadensis, Fragaria virginiana* Duchesne var. *glauca* S. Wats., *Lupinus* sp., *Pedicularis bracteosa* Benth., *Pyrola secunda* L., and *Linnaea borealis* Holtz. var. *americana* (Forbes) Rehder. Mosses, *Brachythecium* spp. and *Polytrichum juniperinum* Hedw. var. *alpestre* B.S.G. Byrol. Eur., and lichens, *Peltigera canina* (L.) Willd. and *Cladonia* spp., are abundant. Forested parts of the parkland have *Picea engelmanni* relatively increased in abundance and *Abies lasiocarpa* decreased, in contrast to the condition in most ranges. The shrub layer is scanty, and is dominated by *Salix* spp., the herb layer is dominated by *Vaccinium scoparium*, but less strongly so than in the forest zone. Treeless openings are of two types: a heath dominated by *Vaccinium caespitosum* Michx. and a "mountain meadow" dominated by *Danthonia intermedia* Vasey, with lesser numbers of *Carex* spp., *Trisetum spicatum* (L.) Richter, *Phleum alpinum* L. and *Sibbaldia procumbens* L.

Montane Forest Region

This is the lower-level forest of dry slopes. It occupies wide areas of the interior of southern and central British Columbia and a narrow zone along the east slope of the Rockies near the United States border. The dominant trees are blue Douglas fir, *Pseudotsuga taxifolia* (Poir.) Britton var. *glauca* (Mayr) Schneid., and lodgepole pine, *Pinus contorta* Dougl. var. *latifolia* Engelm. Ponderosa pine, *Pinus ponderosa* Dougl., is important in the southern interior, especially in drier habitats. To the south, segregation of *Pinus ponderosa* and *Pseudotsuga-Pinus contorta* zones is even more striking, and Daubenmire (1943) treats these as separate major zones. Munro and Cowan (1947) refer much of what is here included in montane forest to the subalpine forest region, using *Pinus contorta* as an indicator of the latter. Halliday recognizes five sections, which are retained for descriptive purposes here.

The *ponderosa pine and Douglas fir section* occupies suitable elevations and exposures in the interior dry belt. This section is characterized by the presence of *Pinus ponderosa* (Fig. 38), particularly at the dry lower levels. The other dominant trees are *Pseudotsuga taxifolia* var. *glauca, Pinus contorta* var. *latifolia* and *Populus tremuloides*. The main shrubs (Fig. 39) are *Shepherdia canadensis* and *Rosa* spp., with *Spiraea lucida* Dougl. also common. *Calamagrostis rubescens* Buckl. is the most common herb; other herbs and dwarf shrubs include *Carex concinnoides* Mack., *Arnica cordifolia, Aster conspicuus* Lindl., *Astragalus*

serotinus Gray, *Fragaria glauca, Lathyrus ochroleucus* Hook., *Arctostaphylos uva-ursi* and *Berberis aquifolium* Pursh. At its lower levels the forest thins out to form an open *Pinus ponderosa* parkland.

The *central Douglas fir section* occupies the lower central parts of the interior plateau: the Fraser, Chilcotin, Bonaparte, and middle North Thompson valleys and the plateaus west and east of the Fraser. *Pinus ponderosa* is absent, and *Pseudotsuga taxifolia* var. *glauca* is the chief dominant, with *Pinus contorta* var. *latifolia* important in burn sequences; *Populus tremuloides* is well distributed. Carl and Hardy (1943) describe a woodland plot near Lac la Hache. This contained *Pseudotsuga taxifolia* and *Populus tremuloides,* a very scanty shrub layer with *Shepherdia canadensis, Rosa sayi* Schwinitz, *Salix bebbiana* and scattered mats of *Arctostaphylos uva-ursi,* and a rich herb layer with the grass *Oryzopsis asperifolia* Michx. much the most plentiful species, and with such forbs as *Antennaria parvifolia* Nutt., *Fragaria glauca, Vicia americana* Muhl., *Lathyrus ochroleucus,* and *Erigeron* spp. numerous. Grassland and alkaline marsh and flat communities are also present in this region. Munro and Cowan give some additional notes on the region: lakeshore vegetation, with *Populus tremuloides, P. trichocarpa* Torr. & Gray, and *Alnus sitchensis* Sarg., is characteristic. Bogs or muskegs with *Picea mariana, Betula glandulosa,* etc. are common.

The *northern aspen section,* occupying a territory north of Quesnel, is closely similar to the preceding, but *Populus tremuloides* seems to be more important in it.

The *montane transition section,* extending from Prince George to Hazelton, contains much *Picea engelmanni* and *Abies lasiocarpa,* mixed with *Pseudotsuga taxifolia;* the latter species is believed by Halliday to have been much better represented formerly. *Populus tremuloides, Betula papyrifera,* and *Pinus contorta* occupy extensive territory following fires.

The *Douglas fir and lodgepole pine section* occupies the east slope of the Rocky Mountains in a narrow zone in the Waterton Lakes and Banff regions, reaching its northern limit in the latter area. *Pinus contorta, Pseudotsuga taxifolia* var. *glauca,* with some *Picea engelmanni* and *Pinus flexilis* characterize this section. Larsen (1930) notes the following as common plant associates of climax forest in the Montana equivalent of this section: *Delphinium cucullatum* A. Nels., *Geranium viscosissimum* Fish. & Meg., *Geum triflorum* Pursh, *Festuca ovina* L., *Agropyron tenerum* Vasey, *Bromus porteri* Nash, *Mertensia ciliata* (James) G. Don, *Thalictrum occidentale* Gray, *Potentilla fruticosa* L., *Vaccinium scoparium,* and *Cercocarpus ledifolius* Nutt.

Coast Forest Region

This long, narrow region occupies most of the Pacific coast of North America from central California to Kodiak and the base of the Alaska Peninsula. Though the climax dominants vary somewhat in this long course, the general uniformity of the region is very striking. This is an area of dense, lofty coniferous forests, with moist, dark floors, on which deciduous trees of moderate size and well-developed shrub, herb and moss layers flourish. The principal dominants in Canada are *Thuja plicata* and *Tsuga heterophylla,* with *Pseudotsuga taxifolia* in the south and *Picea sitchensis* (Bong.) Carr. in the north. Associated species include *Tsuga mertensiana, Chamaecyparis nootkatensis* (Lamb.) Spach, and in the south *Abies grandis* (Dougl. ex G. Don) Lindl. The shrubby layer is well developed and includes such species as *Gaultheria shallon* Pursh, *Vaccinium parvifolium* Sm., *Oplopanax horrida* (Sm.) Mig. and *Rubus spectabilis* Pursh.

Fig. 39. Interior of montane forest, Paul Creek, at Pinantan, B.C.. Science Service.

Seral communities include *Pseudotsuga taxifolia* consocies and an associes of *Acer macrophyllum* Pursh, *Alnus rubra* Bong. and *Populus trichocarpa*. Halliday divides the region into four sections.

The *southern coast section* shows the best development of forest. Here the main association is of *Thuja plicata* and *Tsuga heterophylla*, with *Pseudotsuga taxifolia* and *Pinus monticola* Dougl. as secondary species. *Abies amabilis* and *Tsuga mertensiana* appear at higher altitudes and *Abies lasiocarpa* appears near tree line. There has been serious destruction of forests by fire and lumbering in this section.

Seral communities of the section have been studied in an excellent paper by Cowan (1945). He distinguishes three communities in the hydrosere and five in the xerosere. Hydrosere communities are: (1) mud-flat community—rush-sedge-quillwort (*Juncus-Carex-Isoetes*) associes; (2) sedge-meadow community—sedge-water parsley (*Carex-Oenanthe*) associes; and (3) alder-willow community—alder-willow (*Alnus-Salix*) associes. Xerosere communities are: (4) rock-bluff community—moss-hairgrass (*Polytrichum-Aira*) associes; (5) new-burn community—willow herb-groundsel (*Epilobium-Senecio*) associes; (6) coniferous pioneer-forest community—Douglas fir-salal (*Pseudotsuga-Gaultheria*) associes; (7) deciduous pioneer-forest community—madrona-spiraea-salal (*Arbutus-Spiraea-Gaultheria*) associes; and (8) coniferous subclimax-forest community—Douglas fir subclimax-forest community—Douglas fir subclimax (*Pseudotsuga*) consocies. Details and good illustrations are given in Cowan's excellent paper.

The *central coast section*, between Knight Inlet and Douglas Channel, has poorer growth conditions because of lower temperatures and greater exposure. The main association is of *Thuja plicata*, *Tsuga heterophylla* and *Abies amabilis*.

In exposed situations the trees are scrubby and *Chamaecyparis nootkatensis* and *Tsuga mertensiana* are present. *Abies lasiocarpa* occurs at higher altitudes and *Pseudotsuga taxifolia* locally in sheltered valleys.

The *northern coast section* is characterized by an association of *Picea sitchensis, Tsuga heterophylla* and *Thuja plicata* (Figs. 40, 41). *Abies amabilis* occurs on the mainland, but not on the Queen Charlotte Islands. In less favourable sites *Chamaecyparis nootkatensis* and *Tsuga mertensiana* also occur. *Pinus contorta* occurs in poor sites and in the burn sequence.

The *madrona-oak transition section* occupies the islands of the southern Strait of Georgia and part of the adjacent mainland. The characteristic trees are *Arbutus menziesii* Pursh and *Quercus garryana* Dougl. These form a climax community in some places, but in others are seral to coniferous forest. *Cornus nuttallii* Audubon, *Acer macrophyllum, A. circinatum* Pursh and *Rhamnus purshiana* DC. are well-distributed trees and shrubs, often forming a broad-leaved association. Flowering plants are abundant, and include *Erythronium grandiflorum* Pursh, *Camassia quamash* (Pursh) Wats., *Dodecatheon latifolium* (Hook.) Piper, *Fritillaria lanceolata* Pursh, *Collinsia grandiflora* Dougl., *Trillium ovatum* Pursh and *Plectritis congesta* (Lindl.) DC. The introduced *Cytisus scoparius* (L.) Link has occupied extensive tracts.

Munro and Cowan (1947) separate from this a Puget Sound lowlands area, mainly in the delta of the Fraser River, and with its vegetation mostly of recent development following the clearing of conifer forests. Except for the absence of *Arbutus menziesii* and *Quercus garryana* the association dominants are much as in the rest of the section. An associate shrubbery of *Corylus rostrata* Ait. var. *californica* A. DC., *Philadelphus lewisii* Pursh var. *gordonianus* (Lindl.) Jeps., *Rosa nutkana* Presl. and *Cornus californica* C.A. Mey. var. *pubescens* (Nutt.) Jeps. is considered characteristic.

The madrona-oak section as a whole is a xeric community formed in the rain-shadow of Vancouver Island and the Olympic Mountains. Its two characteristic species belong to the Sierran division, otherwise unrepresented in Canada, of the montane forest. However, its floristic and seral relationships to the coast forest are obvious, and Halliday's placement of it as a transitional section associated with the latter seems satisfactory.

Columbia Forest Region

The eastward extension of ranges along the zone of storm tracks that penetrates the broken mountain wall of Washington and southern British Columbia has already been mentioned. The effect of this is to produce on the western slopes of the high interior mountains a zone of forest with many of the characteristics of the coast forest region. The present region was in fact included by Clements and Shelford (1938) in the coast forest region, partly on the ground of a supposed continuity between them along the British Columbia-Washington border. There is really an approach rather than a continuity in British Columbia, and Shantz and Zon's (1924) map suggests that there is no direct continuity in northern Washington either; in view of the differences in forest composition Halliday's separation of the Columbia forest as a distinct region is followed here. Daubenmire points out that the Columbia forest differs from the other forest zones of British Columbia in that it has a very limited range from north to south, whereas the others are all typical over a large part of the length of the Cordillera. Altitudinally this forest occupies a position between the subalpine forest and the montane forest.

Fig. 40. Coast forest, Skeena R., B.C. Science Service.

In Canada the Columbia forest occupies the interior wet belt of British Columbia, especially the main valleys of the Columbia River system in the Selkirk and Monashee mountains, the upper valleys of the Thompson River system in the Monashee and Cariboo mountains, the Quesnel Lake area and the valley of the upper Fraser River between the Cariboo and Rocky mountains. In southern valleys and on middle slopes the dominants are *Pinus monticola* and *Larix occidentalis* Nutt., with an admixture of *Pseudotsuga taxifolia* var. *glauca* and *Abies grandis*. *Thuja plicata* and *Tsuga heterophylla* increase towards the north, while *Pinus monticola*, *Larix occidentalis* and *Abies grandis* decrease. On the basis of these differences Halliday recognizes a southern and a northern section.

Tundra Formation

The tundra formation occupies all parts of Canada that lie north of or above tree line. The essential characteristic of the formation is the absence of trees; however, some treeless areas show characteristics of more temperate regions and from certain standpoints are best considered subarctic or subalpine. The most conspicuous examples lie outside our territory, in southern Greenland, the Aleutian Islands, and the Presidential Range of New Hampshire; but the upland barrens of Cape Breton and probably large treeless areas of Newfoundland appear to fall in the same category.

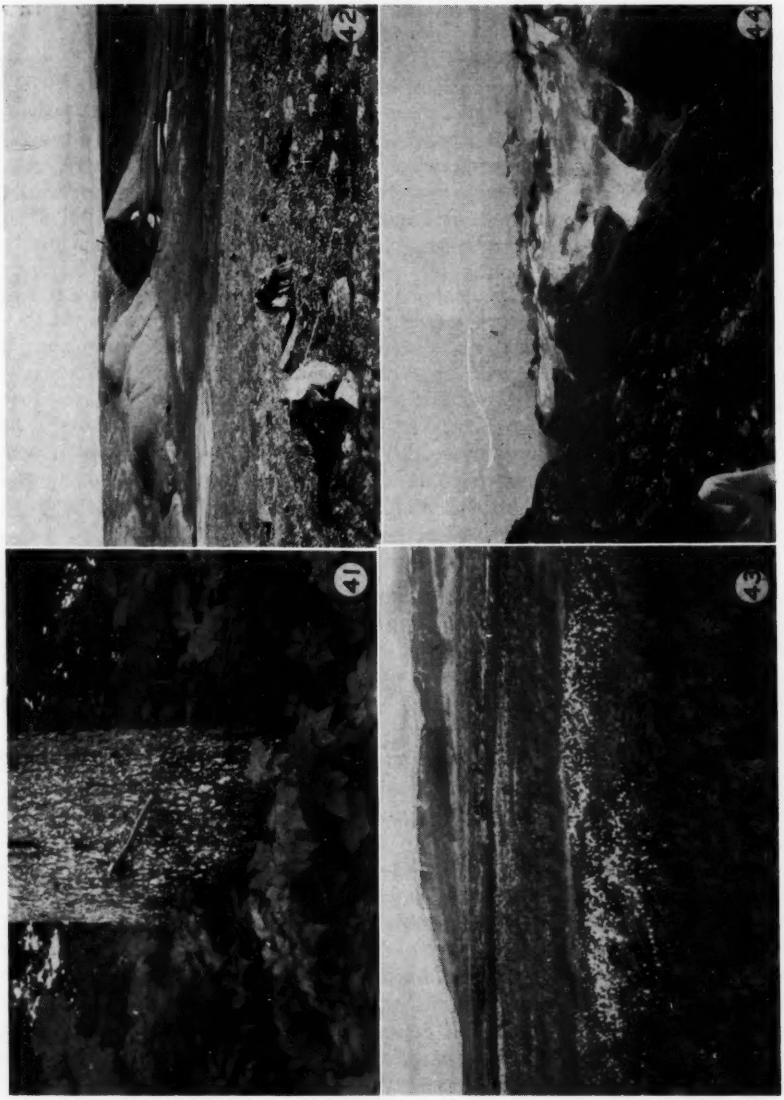
The tundra formation of Canada is easily separated into two regions: the *arctic* and the *alpine*. Environments of these regions are alike in that they are cold and exposed, with a short growing season interrupted by frequent frosts, and with the consequences of scanty vegetation, immature soils, and disturbance by frost; but as well as having resemblances they differ in important respects. The first of these is insolation. Arctic environments have very long days or even perpetual daylight during the growing season, with a

corresponding period of darkness in the winter. Alpine environments, on the other hand, have the normal temperate-zone alternation of day and night. However, the intensity of alpine insolation reaches higher levels, because of the greater altitude of the sun and because of the smaller filtering effect of the rare upper atmosphere. The intensity factor tends to be offset by the cloudiness of mountain peaks. A second difference is in precipitation, which is low in the arctic, but often very high in the alpine region. A third and important difference is the presence of permafrost in the arctic and its absence from the alpine region. A fourth difference is in accessibility from adjacent regions. Arctic habitats are usually widely separated from temperate regions, whereas alpine habitats may be separated by only a few thousand feet, and upward displacement may be facilitated by updrafts or tactic movements. Alpine habitats, therefore, are much more open to contamination by temporary invaders from temperate zones than are those of the arctic. A fifth difference is in degree of contact with similar habitats. Arctic habitats typically are continuous or irregularly dispersed over wide areas; alpine habitats. on the contrary, are usually restricted and isolated, often severely so. They tend to show the same phenomena of local extinction and endemism, both relict and adaptive, that give an irregular aspect to insular faunas of all kinds. In addition to all these environmental differences, there is the factor of isolation between the alpine and arctic regions; in North America they now have a comparatively narrow junction, at one end of the linear and interrupted area of the alpine region, and in a very narrow sector of the broad arctic region. In the recent past it is possible that even this narrow connection was at times severed.

Because of these partly opposed factors of semi-isolation and habitat resemblance and difference, we would expect to find both similarities and differences in flora and vegetation. This expectation is fulfilled. Daubenmire (1943) compares alpine and arctic floras, largely on the basis of data from Rydberg (1913, 1914, 1916). The alpine flora of the Rocky Mountains consists of four elements: (1) species not confined to the tundra formation; (2) species common to alpine and arctic regions; (3) endemic species of the alpine region whose nearest relatives are in lower and warmer adjacent regions; (4) endemic species of the alpine region whose nearest relatives are in the arctic region. Groups 1, 2 and 4 decrease northward, group 3 increases northward. Many of the communities of the two regions are similar, though often differing in species composition; others no doubt are structurally different; detailed comparisons are difficult in the present state of knowledge.

Arctic Region

So far as Canada is concerned this includes all areas beyond the northern limit of trees. To this may conveniently be added the treeless mountain summits of the Gaspé Peninsula and possibly certain summits in Newfoundland and in eastern Quebec north of the St. Lawrence River. The coastal strip of Labrador has a mixed character in its southern part. A treeless zone characterized by some arctic species rounds the corner to the north shore of the Gulf of St. Lawrence and extends along it for some distance. The mountains of Gaspé are well known for their numerous endemic elements (Fernald, 1925; Marie-Victorin, 1938), but modern research suggests that this individuality is part of the general problem of Gulf of St. Lawrence endemism and does not represent a specifically alpine feature (Wynne-Edwards, 1937; Scoggan, 1950). In both east and west the arctic region sends peninsulas southward into the



Figs. 41-44. Fig. 41, Coast forest: undergrowth beneath Sitka spruce, Skeena R., B.C. Fig. 42, *Saxifraga oppositifolia* barrens, Alert, Ellesmere I. Courtesy P. Bruggemann. Fig. 43, Marshy tundra, with *Eriophorum* sp., near Eureka, Ellesmere I. Courtesy P. Bruggemann. Fig. 44, Alpine zone, interior of British Columbia, showing rock-barrens with crustose lichens. Courtesy J. D. Gregson.

subarctic along high or exposed tracts of land. In the west these form a transition of largely unknown character to the alpine zone of the Cordillera. An important borderline exists at the edge of the range of *Abies lasiocarpa* in the southwestern Yukon (Porsild, 1951). Transitional features are assumed to occupy a considerable area in the Yukon and northern British Columbia, but no full survey has been made.

Despite the greater accessibility of the arctic since the advent of air transport, our knowledge of the vegetation is imperfect. Even the factors that control the boundaries of the region are poorly known. Dansereau (1955) considers the following lines important in determining the distribution of tundra: (1) the isotherm of 10°C. for the warmest month, (2) the Nordenskiöld line, and (3) the southern limit of continuous permafrost. Marr (1948) finds that the limit of trees is controlled by edaphic factors on the east coast of Hudson Bay; Daubenmire (1956) considers temperature the main limiting factor in the Rocky Mountains; Porsild (1937) says that insufficient summer precipitation and extreme winter dryness determine the absence of trees over a large part of the barren grounds or tundra. On the whole Raup's (1955) statement about the forest-tundra border is perhaps the safest: "At present, however, this boundary is little more than an observed fact, for we do not have a clear idea of why it occurs where it does. It is presumed to reflect a climatic boundary, but how the climate differs on either side of it and how the difference affects the growth of trees is very little known."

The vegetation of the arctic region as a whole shows considerable variation. Two sets of factors are involved: climatic and floristic. The main climatic features are seen in the maps already presented. There is a great increase in severity of cold from south to north, accentuated in the central part of the region; there is in general a decrease in precipitation from east to west. Floristic factors depend on barriers and centres of dispersal; the latter are partly controversial and cannot be fully discussed here, but the effects are very evident. The most important barriers are the straits and sounds that isolate the Arctic Archipelago. The flora of the southern part of the Archipelago is markedly poorer than that of the opposite arctic mainland (Porsild, 1955). The flora of the northern half of the Archipelago is in turn markedly poorer than that of the southern half, though to what extent this is due to isolation and to what extent to adverse climate is perhaps conjectural. The isolation appears to work both ways, for of the 327 species recorded by Porsild from the Archipelago, only 241 are known from the Yukon, 271 from Mackenzie, 209 from Keewatin and 236 from Ungava. A second barrier is Hudson Bay, which divides the mainland arctic into two sectors; its significance, although noticeable, is less than might be expected. A barrier of major importance is the Mackenzie delta, not so much because of its impassability as because of its position between two great centres of biotic dispersal, the North American arctic on the east and Beringia on the west. There are, then, three main phytogeographic divisions of the Canadian arctic, following Porsild (1955): (1) the Arctic Archipelago; (2) the continental Northwest Territories, Ungava and Labrador and (3) the Arctic Yukon, a portion of the Alaska-Yukon division. Further subdivision is possible, but Porsild states that it would be difficult and in many cases arbitrary.

The most extensive account of plant communities in the Canadian arctic is that of Polunin (1948), who surveys vegetation types in a number of representative localities in the eastern arctic. For full information Polunin's

very clear and detailed paper must be consulted in the original. However, some generalizations are possible. As would be expected, floras and communities increase progressively in richness and variety from northernmost Ellesmere Island (data from Bruggemann and Calder, 1951) to Ungava. Associations restricted to sheltered places at high latitudes become characteristic of higher and more exposed sites southward, and the more protected sites are occupied by richer associations. Communities from the west side of Hudson Bay fit in their general aspect into the series but equivalent associations are appreciably richer in species (Shelford and Twomey, 1941; McClure, 1943; Polunin, 1948).

Even the northernmost land areas have a noticeable amount of plant life. Bruggemann and Calder list 56 species of vascular plants from northern Ellesmere Island at 82°30′N. In this desolate region most of the land lacks closed vegetation. Much of the area is composed of barren stony soil with active frost polygons, in the crevices of which occurs a scanty flora of *Festuca baffiinensis* Polunin, *F. brachyphylla* Schultes, *Luzula nivalis* (Laest.) Beurl., *Juncus biglumis* L., *Draba* spp. and *Saxifraga caespitosa* L. Such extremely barren land is found only in very exposed or otherwise unfavourable situations farther to the south. Somewhat more favourable sites, e.g., gentle, north-facing slopes along the coast, are occupied by *Saxifraga oppositifolia* L. barrens (Fig. 42); cushions or mats of that species occupy as much as half the area, and are interspersed with widely spaced grass-tufts, *Papaver radicatum* Rottb. and *Draba* spp. The *Saxifraga oppositifolia* barren is an important habitat of uplands and exposed lowlands in southern Ellesmere Island, Devon Island and northern Baffin Island. Still more favourably dry sites in northern Ellesmere Island are occupied by barrens or half-barrens of *Dryas integrifolia* M. Vahl. A *Dryas integrifolia* barren, with the associated silvery moss *Rhacomitrium lanuginosum* (Hedw.) Brid. and *Cetraria* spp. and other lichens, is an important habitat in Devon Island and northern Baffin Island, occupying dry lowland areas in the former and hillsides and exposed lowlands in the latter. Farther south it occurs in exposed, xeric areas – crystalline limestones in southern Baffin Island and steep slopes in Ungava. The *Dryas integrifolia* half-barren is the highest community of the xeric series represented in northern Ellesmere Island, but farther south additional members occur. In southern Ellesmere Island, *Cassiope tetragona* (L.) D. Don forms restricted closed communities in sheltered places on *Saxifraga oppositifolia* or *Dryas integrifolia* barrens. A considerable variety of phanerogams, mosses and lichens occur in this *Cassiope* heath. Farther south the *Cassiope tetragona* heath occurs mainly as a zone in the late-snow community. In Devon Island and northern Baffin Island a heath of *Vaccinium uliginosum* L. var. *alpinum* Bigel., with *Cassiope tetragona* and other species, along with *Aulacomnium palustre* (Web. & Mohr.) Schwaegr., *Sphagnum teres* Angst., and other mosses, and *Cetraria islandica* (L.) Ach., *Cladonia* spp., and other lichens, occupies protected, well-watered and well-drained sites. Essentially similar blueberry-lichen heaths, though with added secondary species, occur as far south as Ungava, and reach perhaps their highest development in the tundra phase of the subarctic region. Additional types of heath and scrub occur. In central Baffin Island a moister type has *Ledum palustre* L. var. *decumbens* Ait. as an added species and an increased proportion of mosses. In southern Baffin Island a dry heath on acid hilltops has as most important species *Salix uva-ursi* Pursh, *Carex bigelowii* Torr., *Hierochloë alpina* (Sw.) R. & S., *Luzula nivalis*, *Vaccinium* spp., and *Cladonia* spp. A dry heath with *Vaccinium uliginosum* var. *alpinum*, *Arctostaphylos alpina* (L.) Spreng., *Carex bigelowii* and

lichens occurs in northern Ungava. In southern Baffin Island and northern Ungava the richest type of shrub community is a *Betula glandulosa* Michx.-*Salix cordifolia* Pursh var. *callicarpaea* (Trautv.) Fern. scrub, with only a few associates, e.g., *Calamagrostis canadensis* var. *scabra* (Presl) Hitchc. Dry grassy or grass-lichen environments also occur. A *Luzula-Heirochloë-Salix herbacea*-lichen association is recorded from central Baffin Island. In southern Baffin Island is found a heathy meadow of *Dryas integrifolia, Carex rupestris* All. and other species of *Carex*, together with mosses and lichens, especially *Cetraria* spp. and *Cladonia* spp. In Ungava occur an upland community of *Luzula* and *Hierochloë* in a moss mat composed chiefly of *Rhacomitrium lanuginosum*, and on steep sheltered slopes a sward of *Carex canescens* L., *Calamagrostis canadensis* var. *scabra* (Presl) Hitchc., *Carex bigelowii*, and other grasses and sedges.

Marshy and wet environments (Fig. 43) form a distinct series, characterized especially by cotton-grasses, *Eriophorum* spp., of which *E. angustifolium* Honck. is the most important. *E. angustifolium* var. *triste* Th. Fries occurs on marshy slopes in northern Ellesmere Island. *E. angustifolium* is associated with *Arctagrostis latifolia* (R.Br.) Griseb. and *Carex* spp. in southern Ellesmere Island, and from Devon Island southward the association is joined by *Carex aquatilis* Wahl. var. *stans* (Drej.) Boott. From Baffin Island south *Eriophorum scheuchzeri* Hoppe and other species join the association as important constituents; in Ungava *Scirpus caespitosus* L. var. *callosus* Bigel. and *Dupontia fisheri* R. Br. var. *aristata* Malte are listed as important additional species. Transitions from marshy to heath habitats exist. Salt marshes have a different flora. *Puccinellia phryganodes* (Trin.) Scribn. & Merr. is the characteristic dominant, occurring sparsely in Ellesmere Island, and in dense communities farther south, where it is associated with *Stellaria humifusa* Rottb., *Carex bipartita* All., var. *amphigena* (Fern.) Polunin, and other species. A strand vegetation is lacking in Ellesmere Island; on Devon Island *Mertensia maritima* (L.) S. F. Gray var. *tenella* Fries appears; farther south this is joined by *Arenaria peploides* L. and *Elymus arenarius* L. *sensu lat.* Between tide-marks in Baffin Island and southward there is usually a well-defined zone of *Fucus* spp. and other algae.

Certain special habitats also require mention. Areas, for instance shaded depressions, where the snow lies very late have a special flora, composed in the outer zone of species that benefit from protection, and inwardly of species that can germinate very rapidly and survive in an abbreviated growing season. In northern Ellesmere Island no such zone was recognized; in southern Ellesmere Island there is a simple flora composed of *Phippsia algida* (Sol.) R.Br., *Saxifraga cernua* L., *S. oppositifolia* and a few other species. On Devon Island *Cassiope tetragona* is the characteristic species. Farther south a concentric spectrum of zones is found. The zones are typically five: an outer zone of rich heath, with *Vaccinium uliginosum*, etc., a zone of *Cassiope tetragona* heath, a zone of *Salix herbacea* L., *S. artica* Pall., *S. reticulata* L., and *Luzula* spp.; then a herbaceous half-barren zone of *Arenaria sajanensis* Willd., *Carex bipartita, Luzula confusa* Lindeb., *Saxifraga* spp., etc., with characteristic snow-patch cryptogams; next a herb-barren zone of such species as *Phippsia algida, Cerastium alpinum* L., *Draba fladnizensis* Wulfen, *Luzula confusa, Saxifraga* spp., etc.; and finally an inner, virtually barren zone, perhaps with *Phippsia algida* and sometimes a few scattered mosses. A second set of communities, associated with manuring, characterizes areas around bird-roosts, animal dens and the like; also in this category are the neighbourhood of Eskimo settlements, musk-ox meadows and the bird-cliffs of certain maritime environments. Polunin describes the bird-cliffs of Wolstenholme graphically. There are two main plant communities:

a dense grassy sward of *Poa artica* R. Br. and other species, developed on a wet squishy humus; and a "patchwork quilt" of lichen rosettes, chiefly *Cetraria* and *Cladonia* spp., on a moss base composed of *Dicranum* spp., *Polytrichum* spp., etc. Bruggemann and Calder describe the flora of bird mounds in northern Ellesmere Island. Certain species are invariably present: *Poa abbreviata* R. Br., *Cerastium alpinum*, *Stellaria monantha* Hultén, *Papaver radicatum*, and *Draba alpina* L. Others occur less regularly. Porsild (1955) describes a number of such eutrophic habitats from the western part of the Arctic Archipelago. He gives a considerable list of plants from owl perches and animal burrows; he notes that falcon nests on cliffs are marked by the abundant growth of a red lichen, *Caloplaca elegans* (Link.) Th. Fries, on the cliff below, accompanied by white dropping-splashes and lush green vegetation on the basal scree; he lists a variety of species from such habitats. He notes a meadow-like vegetation at about 2,000 feet elevation in the interior of Axel Heiberg Island, probably developed in a sort of symbiosis with the musk-ox. A similar development of aquatic and subaquatic vegetation occurs in association with geese, eider ducks and other water-fowl.

In general the habitats described by Porsild from the western Arctic Archipelago are comparable to those of the east. Stony *Dryas* barrens are widespread, as in the northern half of the eastern part of the Archipelago. The characteristic species of these barrens are *Dryas integrifolia*, *Potentilla rubricaulis* Lehm., *Oxytropis arctica* R. Br., and *Kobresia myosuroides* (Vill.) Fiori & Paol. Closed vegetation is mainly in the form of marshy, hummocky tundra. *Arctagrostis latifolia*, *Hierochloë pauciflora* R.Br., *Carex* spp., *Eriophorum angustifolium* var. *triste*, *Salix* spp. and a considerable number of other plants grow on the hummocks; between the hummocks grow *Equisetum variegatum* Schleich., *Alopecurus alpinus* Sm., *Dupontia fisheri*, *Eriophorum scheuchzeri*, *Ranunculus hyperboreus* Rottb., etc. Shore communities are much as in the eastern part of the Archipelago, but strand species are scarce. Late-snow communities are poorly developed because of the low regional precipitation. Snow patches, as opposed to late-snow areas, give protection to shrubby and other species, and are associated with the scattered and restricted heath communities, which are dominated by *Cassiope tetragona* and *Vaccinium uliginosum*. Rarely thickets of *Salix* spp. occur.

Porsild (1937) gives a condensed description of vegetation on the mainland in the Great Bear Lake-Coppermine district. On uplands a lichen-heath is predominant, with such species as *Betula glandulosa*, *Ledum palustre* L. var. *decumbens* Ait., *Arctostaphylos alpina*, *Cassiope tetragona*, *Vaccinium* spp., *Eriophorum* spp., *Pedicularis* spp., *Lupinus nootkatensis* Donn, *Oxytropis* spp., and *Rhododendron lapponicum* (L.) Wahl., in a thick mat of lichen and mosses. In wet places grow thickets of *Salix* and *Alnus* spp., with *Castilleja pallida* (L.) Spreng., *Pedicularis lapponica* L., *Pyrola* spp., *Polygonum* spp., *Ranunculus* spp. and *Habenaria obtusata* (Pursh) Richardson. Bottom lands are clothed with extensive meadows, poor in species, with grasses and sedges forming about 75 per cent of the cover. Sandy ridges have a rich flora due to manuring by the Parry ground squirrel, *Citellus parryi* (Richardson). Rank grasses are mixed with *Papaver nudicaule*, *Erysimum pallasii* (Pursh) Fern., *Taraxacum* sp., *Polemonium boreale* Adams, etc. In rocky places there are lichen barrens, with crustose lichens and a crevice flora that includes *Saxifraga* spp. and the three arctic ferns, *Woodsia glabella* R.Br., *W. ilvensis* (L.) R.Br. and *Dryopteris fragrans* (L.) Schott. *Dryas-Empetrum* heaths or half-barrens occur where there is a little more soil, with various herbaceous species associated.

Porsild (1945) discusses briefly the vegetation and flora of the east slope of the Mackenzie Mountains along the Canol Road. These mountains are forested at lower elevations, but at higher elevations an arctic flora with some alpine components is found. On the Plains of Abraham, an area of rubble-covered fragmented limestone with active polygons, solifluction and stone creeps, *Saxifraga oppositifolia-Dryas integrifolia* barrens occupy most of the surface. On gentle, sheltered slopes grows a *Cassiope tetragona* heath. On sheltered level places, terraces, etc. occurs an association of *Arctagrostis latifolia*, *Puccinellia vahliana* (Liebm.) Scribn. & Merr., *Kobresia simpliciuscula* (Wahl.) Mack., *Juncus* spp. and various forbs. The general region is rich in calciphilous species, and contains many intrusions from the Cordilleran flora.

Raup (1947) gives a somewhat more detailed analysis of vegetation in the vicinity of Brintnell Lake in the southern Mackenzie Mountains. The tundra flora of this region contains a considerable Cordilleran element, though Raup has analysed his data in a way that does not reveal the exact proportion. As is often the case in mountain environments, the different habitats present a confused picture, with much intergradation and intermingling, making schematic interpretation of the vegetation difficult. Raup recognizes six main habitats. (1) Damp alpine "meadows" on fairly stable soil have as primary species a mixture of shrubs, sedges and grasses, forming a closed turf. The primary species include *Salix* spp., *Betula glandulosa*, *Carex podocarpa* R.Br., and *Festuca altaica;* these are accompanied by other sedges and grasses and a wide variety of forbs and small shrubs. (2) Dry alpine "meadows", also on relatively stable soils, present a variety of facies, depending on elevation, exposure and perhaps on substratum. The extreme variants are, on the one hand, a heathy sward of *Dryas integrifolia*, *Cassiope tetragona*, *Festuca altaica*, *Salix reticulata*, *Carex scirpoidea* Michx., *Vaccinium uliginosum* var. *alpinum*, and prostrate *Betula glandulosa*, often with the addition of *Phyllodoce glanduliflora* (Hook.) Cov. and *Empetrum nigrum*, and, on the other hand, a lichen heath of *Dryas octopetala* L. and *Vaccinium uliginosum* var. *alpinum*, on a mat of *Cetraria* and *Cladonia* spp. A considerable range of intergrades and variants can be distinguished. (3) Loose slides, where a considerable number of species with low water needs and adaptable root systems are found. These include, among others, *Woodsia ilvensis*, *Carex* spp., *Luzula* spp., *Salix* spp., *Arenaria* spp., *Draba* spp., *Saxifraga* spp., *Dryas* spp., *Oxytropa* spp. and *Arnica* spp. (4) Mats, festoons and terraces of such species as *Saxifraga tricuspidata* Rottb., *Salix glauca* L. var. *perstipula* Raup, and *Salix artica*, accompanied by mosses and fruticose lichens. (5) A very barren stony polygon habitat with crustose lichens and widely spaced plants of *Saxifraga lyallii* Engler. (6) A ledge and crevice flora of crustose lichens, *Dryas integrifolia*, *Saxifraga tricuspidata*, *Salix glauca* L. var. *acutifolia* (Anders.) Schneider, and *Trisetum spicatum* (L.) Richter var. *maidenii* (Gand.) Fern.

Porsild (1951) describes several localities above tree-line on the Yukon side of the Canol Road. A pronounced floristic break exists at the Mackenzie-Yukon divide, a number of calcicolous species being confined to the eastern side, and a number of Cordilleran species being mainly or entirely limited to the western side. Communities here include a grassy scrub of *Betula glandulosa*, *Spiraea beauverdiana* Schneid., *Vaccinium* spp., *Festuca altaica* and other grasses and sedges, with many other species; a terrace and esker scrub of *Betula glandulosa* and *Salix pulchra* Cham., with a small assortment of other species; a gravel-bar community of *Salix* spp., *Dryas integrifolia*, etc.; and a "bog" community including *Eriophorum angustifolium*, *E. scheuchzeri*, *Carex stans*, *Kalmia polifolia* Wang var. *microphylla* Hook., *Ledum groenlandicum*, etc.

Farther to the southeast, on the Pelly Plateau, the vegetation of the Mt. Sheldon area is considered by Porsild to include relict elements. Oxylophytic and calciphilous, wet and dry communities are found in this area, and Porsild gives an extensive list of species. On the north side of the Pelly Mountains a calcareous formation harbours an extensive series of calciphilous plants; this area is sharply marked off from the main body of the range, in which non-calcareous rocks predominate. In the calcareous zone, dry *Populus tremuloides-Juniperus communis-Arctostaphylos-Viburnum* scrub occupies dry south-facing slopes; on moist slopes a mossy heath of *Betula glandulosa, Salix reticulata* and various Ericaceae and grasses occurs. In the non-calcareous zone rich alpine herb-mats and flower gardens, with over 100 species of vascular plants, occupy well-watered, south-facing slopes; gravelly, late-snow areas have lichen heaths, with *Salix* spp., *Betula glandulosa,* and *Cassiope tetragona* (L.) D. Don ssp. *saximontana* (Small) Porsild.

Halliday's map shows the entire tundra area of the Mackenzie and Pelly mountains as isolated from the main body of arctic tundra. There are many alpine and Cordilleran features in the communities just described from that area, and there would be advantages in referring them to the alpine region. However, in the present scanty state of knowledge of northern British Columbia, the Liard River makes a convenient boundary floristically as well as physiographically.

Porsild (1951) divides the Yukon into seven phytogeographic provinces, of which the arctic-alpine element of the southeastern province has just been discussed. Of Porsild's other provinces the following have important arctic-alpine sections: the St. Elias Range, the western Yukon Plateau, the Richardson and British mountains, and the Arctic Coastal Plain. Some of these areas are poorly known, others (Coastal Plain, St. Elias Range, Yukon Plateau) are rich in Beringian and/or endemic species (Porsild, 1951; Hultén, 1941-50; Anderson, 1943-45). Vegetational information on the Arctic Coastal Plain is given by Johansen (1926); recent work in the Barrow-Umiat region of Alaska (e.g., Churchill, 1955) probably also has considerable application to this area.

Alpine Region

A general account of alpine communities in the Cordillera is given by Weaver and Clements (1938). They distinguish between the Petran tundra of the Rocky Mountains and the Sierran tundra of the Sierra Nevada and ranges in the coastal zone farther north. These are similar in general composition but their dominant and subdominant genera are often represented by different species in the two sections. Unfortunately the data on which their classification is based are drawn largely from the U.S.A., and the degree to which it is applicable in Canada has not been established by any comprehensive survey. Munro and Cowan (1947) make a transverse division in British Columbia at the level of the Skeena and Peace rivers, and recognize northern and southern alplands divisions. This agrees with Daubenmire's (1943) boundary between northern and far-northern divisions of the Rocky Mountains. The floristic differences between northern and southern alplands are poorly known, but they have several distinct species-pairs in mammals. These systems may be combined to give a threefold division of the alpine region of Canada, into northern alplands, southeastern alplands and southwestern alplands.

The *northern alplands section* consists of extensive areas in the Cassiar, Skeena and Omineca mountains and in the northern parts of the coast range and the Rocky Mountains. The alpine areas are more extensive and less isolated than in

the southern alpland sections. According to Munro and Cowan the flora is believed to be closely similar to that of the southern alplands, but no precise information is available.

The *southeastern alplands section* is perhaps the best known. Daubenmire (1943) briefly describes a number of communities in a general description of the Petran tundra. *Boulder fields* (Fig. 44) have crustose lichens on the frost blocks and a crevice flora of such plants as *Oxyria digyna* (L.) Hill, *Aquilegia* spp., *Polemonium* spp., *Penstemon fruticosus* (Pursh) Greene and *Sibbaldia procumbens* L. *Fell fields*, i.e., boulder fields with the interstices filled with coarse soil, are characterized by a sparse vegetation of cushion plants such as *Silene acaulis* L., *Dryas octopetala, Arenaria sajanensis* Willd. ex Schlecht., *Erigeron* spp., *Luzula spicata, Paronychia* spp., *Phlox caespitosa* Nutt, and *Selaginella densa* Rydb. Further development of soil leads to the formation of climax "*alpine meadow*" (Fig. 45). *Carex* spp., *Kobresia bellardii* (All.) Degl., *Poa* spp., *Phleum alpinum, Deschampsia caespitosa* (L.) Beauv., *Trisetum spicatum* (L.) Richt., *Agrostis* spp., *Festuca* spp., *Polygonum viviparum* L., *Potentilla* spp., *Geum turbinatum* Rydb., *Trifolium* spp., and *Pedicularis parryi* A. Gray are common dominants. Hydroseres are varied and include communities dominated by species of *Carex, Eleocharis, Salix, Trollius, Caltha, Ranunculus* and *Menyanthes.* Examples of endemic species derived from lower zones, endemic species derived from the arctic region and widespread species are given by Daubenmire. Weaver and Clements' description of the climax meadow is essentially similar to that of Daubenmire.

Shaw (1916) gives a more detailed description of the alpine zone in the Selkirk Mountains. Shrubby communities of alpine meadows are characterized by such species as *Arctostaphylos uva-ursi, Cassiope mertensiana* Don, *Empetrum nigrum, Phyllodoce* spp., *Gaultheria myrsinites* Hook, *Kalmia polifolia* and *Dryas* spp. Very wet sites have such species as *Trollius laxus* Salisb., *Caltha macounii* Green and *Erythronium grandiflorum* Pursh., together with sedges, grasses and and many other plants. Mesophytic alpine meadows are dominated by *Pulsatilla occidentalis* (S. Wats.) Fregn., often with several other species associated. Moraines have a rich flora and extremely varied moisture conditions. Rockslides have an assortment of xerophytes. Late-snow areas are characterized by *Carex nigricans* C. A. Mey., *Petasites frigidus* (L.) Fries and *Caltha macounii.* In the Paradise Mine area of the Purcell Range Carl and Hardy (1945) distinguish several habitats. Stream margins and moist parts of the meadows are overgrown with thickets of *Salix* spp., on the banks of the streams grow *Senecio triangularis* Hook., *Epilobium hornemannii* Reichenb. and *Arnica chamissonis* Less., and on muddy or gravelly flats *Draba praealta* Greene, *Sagina saginoides* (L.) Brit., and *Rhodiola integrifolia* Raf. On rock outcrops were found *Saxifraga* spp. and *Cystopteris fragilis* (L.) Bernh.; on steep slopes grow *Penstemon confertus* Dougl., *Potentilla fruticosa, Aquilegia flavescens* S. Wats., *Saxifraga* spp. and *Epilobium augustifolium.* Well-drained slopes have patches of *Dryas octopetala, Eriogonum subalpinum* Greene and *Cassiope mertensiana.* Exposed summits have *Potentilla nivea* L., *Oxyria digyna, Draba* spp., *Erigeron* spp. and other plants.

The *southwestern alplands section* is characterized by higher precipitation and lower snowline, and alpine vegetation sometimes is completely squeezed out, coast forests abutting on glaciers or snowfields. Carl (1944) gives very brief notes on the alpine zone in the Forbidden Plateau region of Vancouver Island, noting as dominant *Saxifraga tolmiei* Torr. & Gray, *Spiraea pectinata* Torr. & Gray, *Arenaria verna* L., *Erigeron compositus* Pursh, *Phacelia sericea* Gray, *Lomatium martindalei* C. & R. var. *angustatum* C. & R., and *Phlox diffusa* Benth.

Fig. 45. Moist alpine meadow at border of upper subalpine zone, Banff, Alta. *Gryllo-blatta campodeiformis* E. M. Walker was collected under the trees in the background.

V. Fresh-water Environments

Fresh-water environments are of extraordinary importance in almost all parts of Canada. The moderate to high precipitation and moderate to low evaporation make for abundance of running, standing and ground water in most regions. The very large area with gentle relief and immature postglacial drainage has a high proportion of the surface occupied by undrained or partially-drained basins, resulting in an almost unbelievable abundance of lakes and ponds of all sizes. A considerable amount of limnological work has been done in Canada, but the literature is scattered and results of many important projects remain unpublished.

Lotic Environments

The streams and rivers of Canada are remarkable for both their variety and their numbers. The *Canada Year Book, 1952-53* lists 14 major rivers or river system flowing into the Atlantic Ocean, 22 flowing into Hudson Bay, five flowing into the Arctic Ocean, and nine flowing into the Pacific. Of these, six–the St. Lawrence, Nelson, Churchill, Yukon, Columbia and Mackenzie–are 1,000 miles or more in length. Also, the Milk River and several of its tributaries have short courses representing the Mississippi drainage in Canada. Smaller streams, both permanent and temporary, abound in most parts of the country.

The St. Lawrence River system has a length of 1900 miles; and drains about five-eighths of the Atlantic slope of Canada. The St. Lawrence River itself has its head at the discharge of Lake Ontario. It runs as a non-tidal river of large size as far as Lake St. Peter. The upper course contains numerous rapids, some of major size; the last set is the Lachine Rapids at Montreal. Just below Lake Ontario the river course is much divided in the Thousand Islands district. At Montreal the river is a mile wide and deep enough for ships of 20,000 tons. In Lake St. Peter there is a small tide; at Quebec the tide is 20 feet, but the water

is still fresh. At the foot of the Island of Orleans the water is brackish and below this it rapidly approaches full salinity. Several large tributaries empty into the fresh-water part of the course: the Ottawa, draining a large part of western Quebec and eastern Ontario, contributes rather turbid waters above Montreal; the Richelieu, draining Lake Champlain, and the St. Francis, draining southeastern Quebec, enter Lake St. Peter from the south; the St. Maurice enters from the north at Three Rivers; the Chaudière enters from the south just above Quebec. The largest river entering the estuary is the Saguenay, an exceptionally deep and powerful stream flowing out of Lake St. John.

These are all rapid streams, in spite of their size. They flow, at least in their lower courses, through extensive postglacial marine clay and gravel deposits, and consequently are turbid. According to Russel (1903), the St. Lawrence at Montreal contains about 160 p.p.m. of solids, the main cation being calcium, and the main anions carbonate and silicate. Just before its junction with the St. Lawrence, the Ottawa has about 61 p.p.m. of solids, but with much the same proportions as the St. Lawrence. The basins in general are forested, and despite the large volume of snow melted in a short period in the spring there is no extensive flooding, though minor marginal transgression occurs. The rivers are frozen over solidly for several months, except at large rapids, which remain open. The ice may be several feet thick, but the main body of water underneath is not frozen. Ice-jams sometimes cause local flooding in winter or spring. Muenscher (1930, 1931, 1932) describes aquatic vegetation in the upper St. Lawrence and its southern tributaries, but refers primarily to United States waters. Marie-Victorin (1934, 1935) gives notes on the plants of the middle stretch of the river. Dansereau (1945) has made a detailed ecological study of Lake St. Louis, an enlargement of the St. Lawrence near Montreal. Cuerrier, Fry and Prefontaine (1946) give a useful catalogue of the fish of the region.

Dansereau's description of Lake St. Louis is particularly informative. This shallow lake is really only an expansion of the St. Lawrence River, and presents an interesting mixture of lotic and lentic characteristics. There is no thermocline, and much of the area is under five metres in depth. There are large sand bars that emerge during the low-water period in late summer and autumn. Slopes everywhere are gentle and depth-zones correspondingly broad. Dansereau recognizes nine major depth-zones, characterized by plant associations as follows: (1) a zone of spring flooding, characterized by *Ulmus americana* and *Acer saccharum;* (2) a zone of more prolonged flooding, with *Populus deltoides* Marsh., or *Fraxinus nigra* Marsh. and *F. pennsylvanica* Marsh., associated with *Salix* spp.; (3) the middle beach, with *Desmodium canadense* (L.) DC., *Elymus riparius*, and *Potentilla anserina* L. on sandy soil, or *Spartina pectinata* Link and *Lythrum silicaria* L. on clayey soil; (4) the inner beach, with *Xanthium chinense* Mell., *Cyperus esculentus* L., etc. on sandy soil or *Butomus umbellatus* L. on clay; (5) the outermost fully aquatic zone, dominated by *Sagittaria rigida* Pursh; (6) a rush zone, dominated by *Scirpus validus* Vahl and *Eleocharis palustris* (L.) R. & S. var. *major* Sonder; (7) an eel-grass zone with *Vallisneria americana* Michx. and *Potamogeton* spp.; (8) a water-lily zone with *Nuphar* and *Nymphaea* spp., and (9) a deep-water diatometum. A number of variants of the aquatic zones occur under local influences.

Marie-Victorin describes the zonation from upper to lower St. Lawrence. The rapid waters of the upper St. Lawrence, flowing over limestone and sandstone beds, are poor in higher plants, except for *Podostemon ceratophyllum* Michx. This zone is being greatly modified by water-level changes brought about by construction of the St. Lawrence Seaway.

The alluvial zone, between Montreal and Lake St. Peter, is more similar in its general features to Lake St. Louis. There are stronger seasonal fluctuations in depth, with the water spreading a considerable distance over the flat shore-plain in spring and early summer. The influence of ice is very important. Numerous species of *Potamogeton* and a variety of other submerged or floating plants inhabit these quiet, clayey waters. Emergent plants are numerous and form a dense growth including *Alisma plantago-aquatica* L. var. *brevipes* (Greene) Marie-Victorin, *Butomus umbellatus*, *Eleocharis palustris* var. *major*, *Lythrum salicaria*, *Sparganium eurycarpum* Engelm., *Typha augustifolia* L., *T. latifolia* L., *Zizania aquatica* L. var. *palustris* L., *Sagittaria* spp., *Scirpus* spp., and *Equisetum* spp. The beach zones are much as at Lake St. Louis.

The estuarine zone, from the end of Lake St. Peter to L'Islet County, has a special flora, composed partly of characteristic plants such as *Astragalus alpinus* L. var. *labradoricus* DC., *Bidens eatoni* Fern., *Callitriche stagnalis* Scop., *Gentiana victorinii* Fern., *Isoetes tuckermani* A. Br., and partly of species that are not confined to wet places farther west, but that here are confined to the intertidal zone, e.g., *Lilium canadense* L. and *Tovara virginiana* (L.) Adans. In the fully maritime zone a flora of halophytes appears, including such species as *Juniperus horizontalis*, *Poa eminens* C. B. Presl, and *Plantago eriopoda* Torr.

Some of the major tributaries have special characteristics. The Ottawa River valley is remarkable for its number of Champlain Sea relicts, both terrestrial (Porsild, 1941) and riparian. Twinn (1936) describes rock-shelf environments at Ottawa. The Richelieu valley has certain Appalachian elements not found elsewhere.

The large rivers flowing into Hudson Bay and Hudson Strait have mostly not been investigated from the limnological standpoint. The Churchill River is very poorly known, in spite of the considerable amount of ecological work that has been undertaken in the Churchill region (McClure, 1943; Shelford and Twomey, 1941; Twinn *et al.*, 1947; Hocking and Pickering, 1954), and despite its apparent importance as a breeding site for biting flies. The Churchill River at Churchill has a hard bed and carries very little silt. The ice goes out in June, the average date being June 15. Doan (1948) briefly describes the Nelson River near its mouth. In the 70 miles above its mouth the river drops 200 feet to sea level. The flow is large, representing drainage from an area of about 370,000 square miles. The width varies from one-half mile to two miles, and the current velocity is as high as 10 m.p.h. The banks are of limestone or clay; the water is muddy and cold, but several degrees warmer than the brown-stained bog water of small tributary streams. A temperature of 60°F. was measured on August 18. A higher part of the Nelson system, the Saskatchewan and South Saskatchewan rivers, has been studied during work on the black fly *Simulium arcticum* Malloch (Arnason *et al.*, 1949; Cameron, 1922; Fredeen, Rempel and Arnason, 1951; Fredeen *et al.*, 1953; Rempel and Arnason, 1947). This river is broad and turbid, with a sandy or silty bottom, interspersed with rapids. At Calgary the Bow River is rapid, turbulent, and milky, and flows over a boulder-strewn bottom.

The Rivers of the Northwest have been described in useful papers by Wynne-Edwards (1947, 1952); Clarke (1940) gives general notes on the Thelon River, but aside from noting that it freezes in September or October and opens in June, he gives no limnological data. Wynne-Edwards describes the Slave River as muddy, with many shallow bars, populated by willows as described previously. The channel is unstable and changes constantly. The current is three m.p.h. or more. The mud of the Slave River is discharged in Great Slave

Lake, and the Mackenzie River is clear as far as Fort Simpson, where the muddy Liard enters. Water of the two streams can be distinguished for 100 miles downstream from their junction. The Mackenzie (Fig. 4) is continuously navigable, but there are four rapids in its course. It terminates in a delta 100 miles long by 50 miles wide with a very complex network of channels. The Mackenzie has a considerable variety of fish, but limnological conditions and the invertebrate fauna are poorly known.

The headwaters of the Yukon are swift. From Whitehorse to Dawson the current averages six m.p.h. The water is cold; that of the Lewes is clear, that of the Teslin slightly turbid, those of the Pelly and Stewart rivers are muddy, that of the White River is whitened by volcanic ash. Pacific salmon run 1,800 miles up the Yukon River, and there is a considerable variety of other fish.

Information on the Fraser River is given by Foerster (1929) and Ricker (1943). In its lower course this is a large navigable stream with the bottom near shore of fine gravel and sand. The water in summer is turbid. The summer temperature rises as high as 18°C., the pH varies from 7.8 to 8.4.

Information on smaller streams is more plentiful than on large rivers. Ricker's (1934) classification of Ontario streams makes a useful point of departure, and is reproduced, with a few elisions.

A. Creeks. Volume of flow less than ten cu. ft. per sec. on June 1; width less than ten feet.
   1. Spring creeks. Permanent, usually spring fed; maximum summer temperature under 20°C.
      a. Stony bottom, moderate to rapid current, vegetation of aquatic mosses.
      b. Sandy bottom, moderate to rapid current, bare of vegetation.
      c. Mud bottom, slow current, vegetation usually watercress, or none.
      d. Bottom of dead leaves and other vegetable debris, slow current, vegetation of mosses or none.
   2. Drainage creeks. Not spring fed, or far from springs, often completely dry in summer; maximum summer temperature above 20°C., usually much higher.

B. Rivers. Volume greater than ten cu. ft. per sec. on June 1; width greater than ten feet.
   1. Trout streams (Fig. 46). Maximum summer temperature not over 24°C; main piscivorous fish *Salvelinus fontinalis* Mitchill.
      a. Slow trout streams. Mud over most of bottom; slow current; vegetation of *Potamogeton* spp., etc.
         (i) Slow hard waters. Bicarbonate (as $CaCO_3$) more than 100 p.p.m., hardness more than 150 p.p.m.; vegetation including *Chara* but not *Brasenia* or *Nymphaea*; volume of flow on June 1 not more than 100 cu. ft. per sec.
         (ii) Slow soft waters. Bicarbonate (as $CaCO_3$) less than 25 p.p.m., hardness less than 50 p.p.m.; vegetation including *Brasenia* or *Nymphaea*, not *Chara*; volume of flow on June 1 up to 500 cu. ft. per sec.
      b. Swift trout streams. Stony bottom; moderate to rapid current; vegetation of *Cladophora* or aquatic mosses; typical invertebrates Hydropsychidae, Heptageniidae, Simuliidae.
         (i) Swift hard waters. Bicarbonate (as $CaCO_3$) more than 100 p.p.m.,

hardness more than 150 p.p.m.; simuliid larvae moderately abundant; volume of flow on June 1 not more than 150 cu. ft. per sec.

(ii) Swift soft waters. Bicarbonate (as $CaCO_3$) less than 25 p.p.m., hardness less than 50 p.p.m.; simuliid larvae extremely abundant; volume of flow on June 1 up to 500 cu. ft. per sec.

2. Warm rivers. Maximum summer temperature more than 24°C.; volume of flow with no upper limit; principal piscivorous fish Centrarchidae and Esocidae.

a. Stony bottom, moderate to swift current, supporting typically a *Cladophora*-Hydropsychidae-Etheostominae association.

b. Mud bottom, slow current; with a very varied biota, including *Nymphaea*, Unionidae, Catostomidae, and many Cyprinidae.

Ricker gives examples of all these types and discusses the Mad River, a slow hard-water trout stream, in considerable detail. Additional temperature information on this stream is given by Ide (1935). Harkness and Ide (1946) have considered the relations of stream type and insect fauna. The streams of the Mont Tremblant Park, P.Q., (Robert, 1953) most probably fall in the rapid soft-water trout stream group. Such streams are dominant in the Laurentide Park, P.Q., and in Cape Breton, N.S. Farther to the north this classification appears to break down: streams of all sizes and bottom types support simuliids, and the whole aspect of the invertebrate fauna is probably different. Hocking (1950) and Hocking and Richards (1952) give physical data on a variety of streams in the Whitehorse, N.W.T., and Goose Bay, Labrador, areas, and indicate the varied bottom types and temperature and flow characteristics of the black fly habitats. Unfortunately chemical and biotic data are not available from these studies. Probably special northern subtypes of both hard- and soft-water streams can be distinguished. At Knob Lake, northern Quebec, subarctic streams seemed to be inhabited indiscriminately by trout and coarse fish (Munroe, 1949). This is beyond the range of Centrarchidae, but Esocidae are present.

Ricker (1943) classifies some streams of southwestern British Columbia as follows:—

(1) Large rivers at low elevation, with fast current and loose, stony bottom. Examples: Pitt River, cold and muddy because of glacial origin; Chilliwack River, clear except at freshet, usually cold, occasionally as warm as 18°C., pH 7.6 to 8.0; Capilano Creek; Silver Creek; Nooksack River.

(2) Medium-sized rivers, with fast current but fairly stable bottom. These tend to be cooler because they are more heavily shaded and get more of their water directly from high elevation; summer maximum rarely above 16°C. Examples: Alouette River; Frost Creek; Liumchin Creek; Little Liumchin Creek; Canyon Creek, Tanishi Creek; Stave River.

(3) Warm rivers. Sweltzer Creek has summer temperatures up to 23°C. and a pH range of 7.4 to 8.0.

(4) Small creeks, with four subtypes: (i) slow creeks with a large admixture of spring water; (ii) creeks up to 500 feet elevation, usually with gravelly and precipitous reaches alternating; (iii) similar creeks at middle elevations (about 2,500 ft.) (Fig. 39); (iv) creeks at high elevation.

Arctic streams are described in some detail by Polunin (1948), though no temperature or chemical data are given. Small rivulets on Ellesmere Island yielded algae and diatoms only; the dry beds of some temporary streams had mosses of several species in their wider parts. Algae of various species and

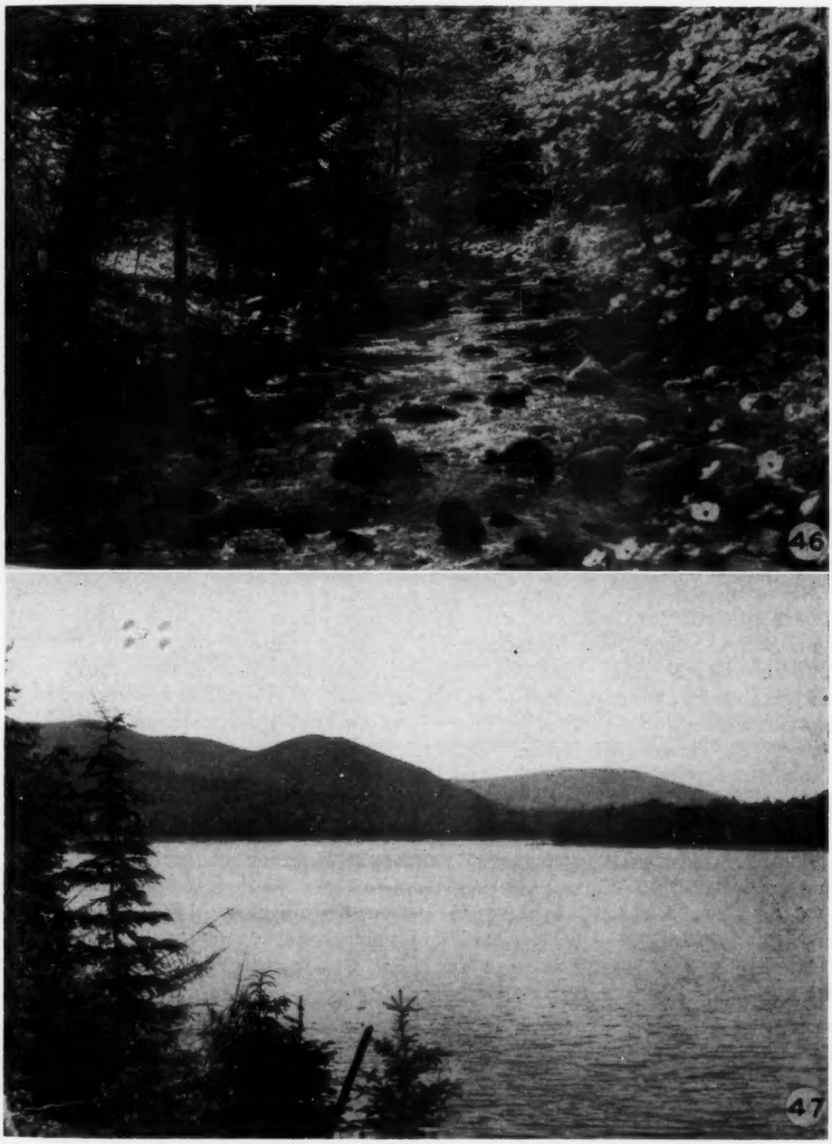
Ranunculus hyperboreus Rottb. were present at Dundas Harbour. A marshy stream at Arctic Bay had over 50 species of algae and diatoms adhering to the marginal sedges. At Clyde River the mosses *Calliergon sarmentosum* Kindb. and *Drepanocladus fluitans* Warnst. occurred, along with numerous algae. The stream flora at Lake Harbour is more diversified, and includes several species of vascular plants. In northern Quebec and Labrador only cursory studies were made. At Chesterfield the stream beds are often abundantly clothed with mosses and there is a rich array of algae. Notes on northern streams in relation to arctic char are given by Grainger (1953) and Sprules (1952).

Lentic Environments

Lakes of all sizes are excessively numerous. The *Canada Year Book, 1952-53* lists 16 lakes of over 1,000 square miles expanse, distributed by provinces as follows: Newfoundland, one; Ontario, six (five partly in the U.S.A.); Manitoba, four; Manitoba and Saskatchewan, one; Saskatchewan and Alberta, one; Northwest Territories, three. Limnological studies have been carried out on the Great Lakes, on Lake Winnipeg, Lake Athabaska, and Great Slave and Great Bear lakes.

Four of the five Great Lakes lie partly in Canada. These are, with areas and greatest depths: Superior, 31,820 square miles, 1,302 ft.; Huron, 23,010 square miles, 750 ft.; Erie, 9,940 square miles, 210 ft.; Ontario, 7,540 square miles, 774 ft. The surfaces of all the lakes except Lake Ontario are at elevations between 570 and 605 feet. Lake Ontario is much lower, at 245 feet. The beds of all except Lake Erie extend below sea level. Lake St. Clair, area 460 square miles, depth 23 ft., forms a natural part of the Great Lakes. Lake Nipigon, area 1,870 square miles, depth 402 feet, is conveniently considered with the Great Lakes, though its elevation is 50 ft. above that of Lake Superior.

Lake Erie, because of its shallowness, especially in the western end, has the most valuable fishery, and has been the centre of intensive limnological work. A recent review with extensive bibliography is given by Langlois (1954) and a comprehensive report of earlier studies by Wright (1955). Lake Erie consists of three main basins: a shallow western basin mostly under 40 ft. in depth, a middle basin mostly less than 60 ft. deep, and a much deeper eastern basin, much of it approaching the maximum depth of 210 feet. The western basin is normally unstratified and homothermal, with summer temperatures about 23°C.; stratification becomes pronounced on rare occasions and may have drastic effects on the bottom fauna (Britt, 1955). The central basin is occasionally stratified, though its bottom temperature is above 4°C. in summer. The eastern basin has typical seasonal stratification with temperatures about 4°C. in the hypolimnion. The waters of the western end are highly turbid, and silt is deposited in large quantities. Sedimentation is thought to have increased greatly since clearing of the hinterland. The Maumee River alone is estimated to have brought over 2,000,000 tons of sediment into the lake in the year 1951. There is visible deposition of silt on aquatic plants and considerable reduction of photosynthesis. Though sedimentation varies seasonally, the bottom deposit consists of an unstratified layer about 6 feet thick, overlying varved postglacial clays. Water levels have a seasonal cycle, being highest in June and July, lowest from November to March. The lake level varies in different years, the range of difference being about five feet. Seiches caused by longitudinal winds may raise water levels by as much as seven feet at one end of the lake, lowering them an equal amount at the other. Pollution has had a local depressing effect on the fauna near some river mouths, and this is exaggerated by the flushing action of seiches. Ice cover forms on Lake Erie almost every winter; wide marginal sheets persist from January to March,



Figs. 46-47. Fig. 46, Rapid stream in coast forest, southern British Columbia. Courtesy J. D. Gregson. Fig. 47, Lake Nictor, head of Tobique R., N.B. Science Service.

but during much of this period there is open water in the middle of the lake. The aquatic vegetation is believed to have decreased greatly in the past 50 years, perhaps mainly because of increased silting and changes in water levels. The aquatic vegetation zones appear to be similar in their general characteristics to those of Lake St. Louis. The main area of biotic productivity is in the shallow western basin. Plankton, benthic Crustacea, Mollusca and Insecta, and a large variety of fish thrive in the lake.

Kindle (1925) describes bottom deposits and biotic zones in Lake Ontario. This lake has fairly clear water; its tributary streams are mostly short, and many of them pass through lacustrine settling basins. However, small streams on the north shore contribute a considerable amount of sediment. There is evidently a thermal stratification, but Kindle gives only scattered measurements. The clay cliffs of the north shore are being cut away rapidly and contribute sediment in this area. Wave action is believed to extend to at least 20 m. depth. Strong currents also are active in the transport of materials. In the Toronto region sand, muddy sand, and gravel deposits in the shallow waters give way to mud at 70- to 100-m. depths. In the Hamilton region there is a shallow-water mud zone enclosed by a sand bar, then muddy sand giving way to mud at greater depths; along the south shore is a zone of bed-rock, boulders and sand. In the Wellington Bay region a wide rock zone is adjoined by sandy mud at about 50 m.; deposits of shallow waters are varied. The profundal zone of the lake bottom seems to be uniformly occupied by soft ooze. Vegetation zones, beginning at the margin, are: (1) a *Typha latifolia* zone in a few centimetres of water; (2) a *Scirpus validus* Vahl. zone in a depth of one to two metres; (3) a *Potamogeton* zone to about 5 m.; (4) a zone of algae and diatoms down to 50 m., with *Cladophora* important in the lower part; (5) the zone below 50 m., with rather scanty microscopic vegetation. Mud from 200 m. has a few diatoms, mainly *Stephanodiscus niagarae* Ehr. Mollusca are largely confined to the zone above eight metres, but *Pisidium* spp. extend far downward. *Mysis relicta* Loven occurs in deeper waters down to about 120 m. The extreme profundal zone is inhabited mainly by chironomid larvae. The marine fish *Triglopsis thompsoni* Girard occurs as a relict in Lake Ontario. Dymond, Hart, and Pritchard (1929), list fishes of Lake Ontario, with a few habitat notes.

We may pass over early work on Lake St. Clair (Pieters, 1894; Reighard, 1894), Lake Huron (Clemens, 1913), and Lake Superior (Agassiz, 1850; Milner, 1874; Smith, 1874; Adams, 1908) and turn to the intensive investigations carried out on Lake Nipigon (Adamstone, 1923, 1924; Bigelow, 1923, 1923a, 1928; Clemens, 1923, 1923a, 1924; Clemens, Dymond and Bigelow, 1924; Dymond, 1926; MacKay, 1924). This large lake has a very long shore line and considerable average depth, the western parts having numerous depths over 70 m. and the eastern part depths up to 130 m. Surface temperatures in July are around 20°C., and there is in summer a pronounced thermocline at depths of from five to 20 m. Transparency with Secchi's disk varied from four to six metres. Oxygen values are in general high. Mollusca are abundant in shallow water and Sphaeriidae extend into the profundal zone; chironomid larvae are massively numerous and maintain high numbers into the profundal zone, other insects are abundant in shallow water. The amphipod *Pontoporeia hoyi* Smith is numerous, especially at considerable depths; the peak abundance is at about 35 m. Oligochaetes occur at all depths, but are most numerous near the surface. Fish are few in species: about 30, as compared with 50 from Georgian Bay and 90 from Lake Erie. *Mysis relicta* is abundant in the open lake waters.

Lake Winnipeg is described by Bajkov (1930) and Neave (1932, 1934). In spite of its large area of 9,398 square miles, this lake differs from those previously mentioned in being very shallow, the maximum depth being about 18 m., and most of the southern part being much shallower than this. The water is very turbid, Secchi's disk readings being under 2 m. The pH varies from 7.6 to 8.4, the lowest values being on the east where neutral or mildly acid tributaries discharge. The lake is highly eutrophic, with phytoplankton of the order of 2 to 20 c.c. per 1,000 l. There are numerous fish species, including many insect feeders. Insect productivity is high.

The major northern lakes have had considerable study, especially in post-war years, because of their potential importance in fish production (Blanchet, 1926; Kennedy, 1949; Larkin, 1948; Miller, 1947; Rawson, 1947, 1950). Great Bear Lake, with an area of 11,800 square miles, is the fourth largest lake in North America. It is very deep: depths of well over 400 m. have been measured and much of the area is over 100 m. deep. It is completely ice-covered from December to June; ice begins to form in October. Surface temperatures are near 0°C. all summer in open water, but close to the shore higher temperatures occur, about 5°C. near Port Radium in July, 13°C. on the west coast in August, and 17°C. in the protected waters of Conjurer Bay. Bottom temperatures are of the order of 4°C. CO_2 is present in very small amounts, O_2 at 85 to 91 per cent of saturation even at nearly 400 m. depth. The pH ranges from 7.2 to 7.4. The water is phenomenally clear, Secchi's disk being visible at depths up to 30 m. The lake is oligotrophic, the plankton being extremely meagre. The bottom fauna is poor and in the open lake does not extend below 20 m. Miller records ten species of fish, the most abundant, in descending order, being lake trout, *Cristivomer namaycush* (Walbaum), cisco, *Leucichthys artedi* (LeSueur), whitefish, *Coregonus clupeaformis* (Mitchill), pike, *Esox lucius* L., and arctic grayling, *Thymallus signifer* Richardson. A considerable proportion of the summer food budget appears to be contributed by terrestrial insects that fall into the water. *Pontoporeia affinis* Lindstrom is limited to depths less than 60 m., primarily because of its concentration in shallow bays. *Mysis relicta* is numerous but its depth distribution has not been studied.

Great Slave Lake has an area of 10,500 square miles; its surface is 495 feet above sea level. It is even deeper than Great Bear Lake; the maximum depth is 612 m.; the mean of the main body of the lake is 35 m.; the greatest depths occur in the east arm. Surface temperatures in the open lake reach a maximum of about 13°C., but in shallow areas reach about 17°C. In McLeod Bay on Aug. 12, 1945, the surface temperature was just over 4°C. Warm water extends only to about 30 m., below which the temperature is 4 to 5°C. The surface is frozen from January to June. Turbidity is variable: Secchi's disk readings are as high as 18 m. in McLeod Bay, as low as 15 cm. in the muddy water of the Slave River delta. O_2 tension is usually more than 80 per cent of saturation. Solids in McLeod Bay are as low as 22 p.p.m. but concentrations are higher near the river discharges. Hydrogen-ion concentrations are close to neutrality. Rawson found 22 species of fish, of which the most numerous are *Coregonus clupeaformis*, *Leucichthys* spp., and *Cristivomer namaycush*. *Pontoporeia affinis* constitutes two-thirds of the bottom fauna and ranges to at least 300 m. depth, though in decreasing numbers. *Mysis relicta* is numerous and also ranges to profundal depths.

Lake Athabaska is smaller, shallower and more southerly than Great Slave and Great Bear lakes. Its area is 3,050 square miles, its maximum depth 130 m., and its mean depth about 27 m. The west end of the lake is warmed rapidly by the Athabaska River and may reach 17°C. by the end of June, when the surface at the middle of the lake is at only about 6°C. By mid-July surface temperatures of 16 to 18°C. are common all over the lake. In shallow water temperatures up to 25°C. occur. The deep water remains cold throughout the summer. The lake is completely frozen by mid-December, and the ice breaks up in early June. Oxygen tension is over 80 per cent of saturation even in deep water; pH varies from 6.6 in the east to 7.7 in the west. Plankton is a little richer than in Great Slave Lake, bottom fauna about the same. *Pontoporeia affinis* is dominant on the bottom; *Mysis relicta* is scarce in this lake. The fish fauna is much like that of Great Slave Lake, with which Lake Athabaska was connected during the glacial retreat.

No general study of the very numerous smaller lakes of Canada has been undertaken. Their number is almost incredible. In an area of 5,294 square miles, accurately mapped, southwest of Reindeer Lake in Saskatchewan, there are 7,500 lakes. Ricker (1932) classifies some Ontario lakes as follows: (1) large lakes, area more than 1,500 square miles (already discussed); (2) acid or soft-water lakes, bicarbonate less than 25 p.p.m.; pH except near surface less than 7.0; typical plant *Eriocaulon*; (3) bog lakes, margined by an encroaching mat of bog vegetation; water always dark brown, acid; bottom of loose silt; (4) hard-water lakes, bicarbonate more than 100 p.p.m., pH greater than 7.0; typical aquatic plant *Chara*. The large lakes have a special fish fauna; in the small lakes an important factor is summer temperature. Lakes that stay cool all summer support speckled trout, *Salvelinus fontinalis*, lakes that are warm in summer may support bass, etc., but not speckled trout. Cutting across both those classifications is the eutrophic-oligotrophic series, discussed by Rawson (1941). Shallowness, high solid content and warmth favour the eutrophic condition. The bog lake appears to be distinguished from the normal oligotrophic lake (Fig. 47) primarily by lack of drainage (Nichols, 1918), though Welch (1935) suggests that this criterion should be treated with caution.

Soft-water lakes are characteristic over a large part of the Canadian Shield, where they alternate with bog lakes. The fauna varies greatly according to geographic location and trophic conditions. Examples of both types are given by Robert (1953, 1955) in his accounts of insect groups in the Mont Tremblant Park. In the Laurentide Park, in extreme Canadian-zone conditions at over 2,500 ft. elevation, highly eutrophic conditions may prevail in sufficiently shallow lakes (Munroe, unpublished data). Langford (1938) discusses the plankton of Lake Nipissing, Ont., and Rawson (1930) the bottom fauna and ecology of Lake Simcoe, Ont. Lake Abitibi and other lakes of the vicinity have been described by Dymond and Hart (1927), Pritchard (1935) and Robert (1944). Lake Abitibi itself is a remnant of glacial Lake Ojibway, whose deposits form the characteristic "clay belt" of the region. Lake Abitibi has a large area (335 square miles) but is very shallow, mostly in the range of two to five metres. The pH ranges from 6.8 to 7.2. Surface temperatures rise to about 20°C. in summer. The water is highly turbid, with Secchi disk visibility about 20 cm. Pritchard describes a variety of plant zones. A number of species of fish are present; the productivity is probably high, but precise information is not available.

Smaller lakes in the region are varied; many are of boggy type, among these Chesney Lake has the bottom about 15 feet deep, and covered with a layer of *Chara* sp. Long Lake, near Lake Nipigon but on the northern drainage, does not show essential faunistic differences from Lake Nipigon (Harkness and Hart, 1927).

Rawson and Moore (1944), in a most interesting paper, compare a range of fresh and saline lakes in the forest, parkland and prairie regions of Saskatchewan. Solids range from 126 to 118,000 p.p.m. Highest salinities occur in the parkland belt (Fig. 48) and parts of the prairie bordering it. In the more arid prairie region temporary saline sloughs or pans are frequent. There are pronounced seasonal changes in salinity caused by evaporation in summer and freezing in winter. In highly saline lakes the main anion is sulphate, the main cations are magnesium and sodium. Salinity makes for lower bottom temperatures and for early spring overturn; it hinders circulation in summer even in the absence of strong thermal stratification. As might be expected, the general abundance of life decreases with increasing salinity; there is considerable selectivity in the responses of different species.

A number of lakes in the Cordillera have been studied (Clemens, Boughton and Rattenbury, 1945; Clemens, Rawson and McHugh, 1939; Brett, 1946; Brett and Pritchard, 1946, 1946a; Rawson, 1934, 1941, 1942; Ricker, 1937; McConnell and Brett, 1946; Neave, 1929, 1929a). There is considerable variation in the lakes of this area. Rawson found Okanagan Lake, area 143 square miles, elevation 1,130 ft., mean depth 69.5 m., greatest depth 232 m., to be a cool, highly transparent, oligotrophic lake, with pH about 8.0, maximum surface temperatures a little over 20°C., and a thermocline or incipient thermocline in the ten- to 20-metre zone. Plankton is moderately abundant, with blue-green and green algae, diatoms, Protozoa, chiefly *Ceratium hirundinella* Müller and *Dinobryon* spp., seven species of rotifers, eleven of Cladocera and three of copepods; the last, however, are numerically very important. The bottom fauna is dominated by chironomid larvae. A shallow muddy bay with emergent beds of *Scirpus* exists at the north end of the lake. Of neighbouring small lakes, Kalamalka, 13 square miles, elevation about 1,300 ft., maximum depth 130 m., is similar in character to Okanagan; Woods Lake, elevation about 1,300 ft., area about four square miles, depth 32 m., is eutrophic, with strong thermocline, depleted hypolimnetic oxygen and black ooze bottom, in contrast to the high hypolimnetic oxygen and clay bottom of the preceding two lakes; Duck Lake, elevation about 1,300 ft., area about two square miles, greatest depth five metres, has abundant plankton and a soft clay bottom, with chironomid larvae and oligochaetes. The surface water is strongly alkaline, pH 8.8.

Rawson (1942) goes on to compare Okanagan Lake with other large lakes in the Cordilleran Region. Key data from this comparison are given in Table 1. There are two types of plankton behaviour; in Okanagan, Minnewanka and Paul lakes plankton fluctuates to comparatively high densities at times during the summer; in the remaining three lakes it remains consistently scarce. Rawson regards the variations in productivity as the resultant of three interacting factors, edaphic, climatic and morphological. Deep, narrow basins, cold climate and low total solids are considered unfavourable; broad, shallow basins, warm climate, and moderately high mineral content are considered favourable.

TABLE I

Selected data from six Cordilleran lakes (Rawson, 1942)

	Altitude (metres)	Area (sq.km.)	Mean depth (metres)	Average duration of open water (months)	Mean Annual Temp. (°C.)	Mean Summer Lake Temp. (°C.)	Mean Summer Temp. of Upper 10 m. (°C.)	Mean Trans-parency (m.)	Total Solids p.p.m.	Bottom fauna dry wt. kg./ha	Net plankton dry wt. kg./ha
Paul	777	3.9	34.2	9.5	5.3	9.4	17.7	13.5	216	36.4	50.2
Bow	1920	3.6	17.6	5.0	0.5	8.3	9.1	0.9	85	2.3	11.9
Waterton	1280	9.6	69.2	9.0	4.0	8.2	12.3	8.0	82	1.7	19.2
Minnewanka	1454	13.0	38.1	8.0	2.2	10.8	15.3	9.8	198	4.5	32.0
Maligne	1663	21.8	40.5	6.5	1.1	6.2	10.8	1.2	104	3.3	20.6
Okanagan	345	370.0	69.5	12.0	7.7	8.6	18.3	9.0	174	2.0	26.0

Subarctic lakes in Ungava have remarkably high fish populations (Munroe, 1949). Limnological studies have not been made, but there is a high density of aquatic insects, especially Diptera. Small shallow lakes in this area are barren except for adventive forms such as water beetles. This is probably the result of total freezing. Bog-rimmed lakes are rare.

Arctic lakes at Churchill, Man., are described briefly by Shelford and Twomey (1941) and McClure (1943). Lakes Isabelle and Annabelle appear to be rather similar. They are shallow and apparently rest directly on permafrost. They contain little vegetation but considerable macroscopic plankton and insect life. Polunin (1948) describes vegetation of a number of lakes in the eastern Arctic. In general the aquatic flora includes only a few phanerogams, among which *Ranunculus* spp. are particularly noticeable. The zone of emergent vegetation is hardly different from ordinary marsh communities. There is a considerable flora of diatoms and other algae, of which Polunin gives numerous lists. Johansen (1922) gives notes on lakes of the Western Arctic. Rawson (1955) summarizes the present status of limnology in the North American Arctic and Subarctic.

Ponds have been studied rather extensively, especially in connection with mosquito control. Unfortunately physical, chemical and biotic information on the waters has not been published in the majority of reports, and we have only gross physical descriptions for many of these environments. Ponds of southeastern Canada can be classified roughly as follows: (1) temporary snowmelt pools, (a) open and (b) wooded; (2) temporary floodwater pools; (3) permanent marshy pools; (4) permanent bog pools; (5) artificial pools. Closely related habitats are (6) tree-holes and (7) *Sarracenia* pitchers.

The fauna of open temporary pools is usually poor, but may include mosquito larvae and other vernal forms. Woodland pools (Fig. 49) persist

Figs. 48-49. Fig. 48, Prairie slough near Qu'Appelle, Sask. Science Service. Fig. 49, Temporary woodland pool near Meach Lake, P.Q. Breeding place of *Aedes diantaeus* H. D & K. and other species. Science Service.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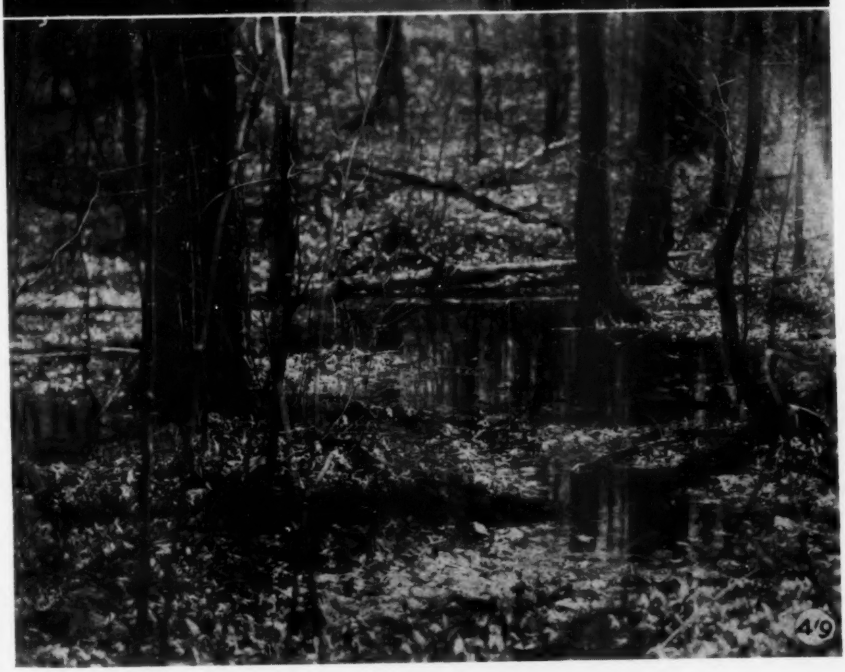
49

longer and have a special biota. This has been described for a Manitoba pool by Mozley (1932). These pools usually have a leaf-covered bottom and clear water, in which plankton multiplies rapidly to great densities. Phyllopods of the genus *Eubranchipus* are among the most characteristic organisms; water mites are numerous, as are numerous adventive insects, especially water-beetles, and a few specially adapted ones, such as the caddisfly *Limnephilus submonilifer* Walker, and the mayfly *Blasturus cupidus* (Say). This is one of the most important habitats for *Aedes* larvae, and they may be found virtually blackening the water as the pools shrink with the advancing season. Larvae of non-biting mosquitoes of the genus *Mochlonyx* are frequent in this habitat. A characteristic amphibian is the frog *Rana cantabrigensis* (Baird).

The classical study of permanent woodland ponds is that of Allee (1912). Though his work was done in northern Illinois, the situations he studied are no doubt paralleled in parts of Canada. He found crustaceans dominant in the pond he studied in spring and autumn, and the snail *Limnaea reflexa* (Say) dominant in summer. A very large variety of insects and some Amphibia and leeches were the largest components of the fauna. Characteristic denizens of permanent woodland ponds are the salamanders of the genus *Ambystoma.*

Features of open permanent ponds are described by Needham and Lloyd (1937). These resemble lakes in their marginal vegetation zones. The emergent zone may have representatives of the genera *Sparganium, Scirpus, Eleocharis, Alisma, Sagittaria, Peltandra, Pontederia, Glyceria,* etc. The intermediate zone has a variety of floating vegetation, including rooted forms such as water-lilies and *Potamogeton* spp., and free-floating forms, especially *Lemna minor* L. Finally is found the submerged vegetation zone, which is also very productive, with species of *Potamogeton, Naias, Ranunculus, Zostera, Chara,* etc. Algae are extremely numerous and varied, and the fauna is likewise extremely rich. Aside from insects there are numerous molluscs, especially gastropods, oligochaete worms, leeches, and a variety of Amphibia and small fish. A useful local study of ponds is that of Smith (1946) on Prince Edward Island.

Bog pools are commonly very acid, pH values as high as 4.0 being normal. The fauna is restricted, insects and Sphaeriidae being among the more conspicuous inhabitants. The vegetation has already been discussed under terrestrial habitats above.

Artificial pools vary greatly according to their physical characteristics, and may simulate a number of different types of natural pools. Walker (1953) points out that artificial ponds are remarkable especially for the occasional abundance of otherwise scarce species that find an unusually favourable niche in the disturbed and juvenile environment. Certain artificial environments such as rain-barrels are, as is well known, closely related to natural tree-holes, the ecology of which has been studied by Jenkins and Carpenter (1946).

Pitcher plants and their associates are discussed by Lloyd (1942). The best-known inhabitant of the pitcher fluid is the sabethine mosquito, *Wyeomyia smithii* Coquillet, which seems to be common wherever the plant grows.

On the prairies an additional pond habitat is supplied by the temporary alkaline ponds or sloughs, already mentioned in connection with alkaline lakes. During the spring these support a variety of insect life.

In southwestern British Columbia Hearle (1926) distinguishes the following types of pools important as mosquito habitats: (1) flooded meadows and open lands; (2) cottonwood flood swamps; (3) permanent pools; (4) temporary pools;

(5) rainwater barrels, etc.; (6) woodland pools; (7) tree holes; (8) marshes; (9) permanent swamps with much matted vegetation; (10) salt marshes and coastal rock pools; (11) pools in the Fraser canyon. He describes and illustrates a number of representative habitats, but gives no precise limnological data.

Information on subarctic and arctic pools is given by Curtis (1953), Hocking, Richards and Twinn (1950), Jenkins and Knight (1950) and Haufe (1952). All the pools fluctuate widely in temperature. Almost all described in detail from Churchill, Man., and Whitehorse, Yukon are somewhat alkaline, with pH ranging from 7 to 8.3. At Churchill pools on tundra and in birch and willow scrub average somewhat more alkaline than those in forested areas, which are about neutral. Dissolved solids varied from 50 to 1,282 p.p.m. at Churchill, two forest pools having low values, one the high one; tundra and scrub pools almost all had solids in the range 100 to 400 p.p.m. In studies at Goose Bay, Labrador, mosquitoes were found in pools of from pH 4.5 to pH 7.5, but precise correlations with pool types are not reported. In the Great Whale River district Jenkins and Knight distinguish seven main types of pools inhabited by mosquitoes: (1) pools in subarctic *Picea-Larix-Betula glandulosa*-lichen forest, often shaded and containing *Picea* branches, water usually stained and acid; (2) *Sphagnum*-heath bog, usually unshaded and very acid; (3) "alpine" sedge-moss pool, on wet upland meadows, clear, shallow and unshaded, reaction about neutral; (4) rock pools with vegetation, water clear to stained, reaction acid to slightly alkaline; (5) bare rock pools, without vegetation, unshaded, water clear to stained, reaction about neutral; (6) oxbow pools in spruce forest, large and deep, water stained and somewhat acid; (7) snow-melt pools, in several types of habitats and with varied vegetation, unshaded, clear, very cold, reaction about neutral.

VI. Glacial and Postglacial History

As the origin and distribution of the northern insect fauna will form the theme of a major symposium at the Congress, no effort will be made to give a comprehensive review here of this large and controversial subject. However, a brief account of certain salient points is necessary to make the distribution types and faunal divisions intelligible.

The basic reference on the geological side is Flint (1947). A very informative paper on Pleistocene biogeography is presented by Deevey (1949); several other valuable reviews appear under the same cover. These two papers have good bibliographies. Other comprehensive references, but with less emphasis on North America, are Zeuner (1950), Woldstedt (1954) and Brooks (1949).

It is a well-known and undisputed fact that during the Pleistocene, and indeed during its latest stage (Wisconsin), the greater part of Canada was covered with ice. There is general agreement that the biota was exterminated in the glaciated areas and greatly reduced in peripheral areas. Points of uncertainty or controversy are: (1) the location and extent of unglaciated areas in Canada; (2) the effectiveness of these areas as refugia and as centres of postglacial dispersal; (3) the extent to which the biota was altered in regions to the south of the ice-sheet; (4) the time-scale, correlation, and many features of the course of the glacial retreat and its phases; and (5) the underlying causes of the Pleistocene glaciation as a whole and of its fluctuations.

The fourth or Wisconsin glaciation in central North America exhibits four substages, according to Flint (Flint's "substage" is equivalent to Zeuner's "stage" and Flint's "stage" to Zeuner's "glaciation" or "interglacial"). The lowest or *Iowan* represents the Wisconsin maximum in Iowa, but was exceeded by the following *Tazewell* glacial substage farther east. The Iowan-Tazewell interval

was of considerable duration and cool-temperate climate. A very thin loess sheet, indicating a short interval, separates the Tazewell from the *Cary* glacial substage. The Cary ice-sheet was thinner, more westerly and less extensive than the Tazewell. A short, cool interval (*Two Creeks* interval) separated the Cary from the final or *Mankato* substage of the glaciation. From the Mankato maximum the ice sheet wasted progressively into the postglacial period.

Subdivision of late Cary and Mankato substages is possible on the basis of developmental stages of the Great Lakes. Details of the lake configurations are given by Flint; for our purpose the relative chronology is the important feature. In the waning Cary substage the following lake phases are represented: (1) Early Lake Maumee; (2) Late Lake Maumee+Lake Saginaw+Lake Chicago; (3) Larke Arkona+Lake Chicago. The development was then interrupted by the Mankato readvance, and recommenced from a condition roughly like that of Phase 2; (4) lakes Whittlesey+Saginaw+Chicago; (5) lakes Wayne+Chicago; (6) lakes Warren+Chicago+Duluth; (7) lakes Lundy+Chicago+Duluth; (8) lakes Erie+Algonquin I+Chicago+Duluth; (9) lakes Iroquois+Erie+Algonquin II; (10) lakes Iroquois+Erie+Algonquin III; (11) lakes Ontario+Erie+Algonquin IV; (12) lakes Ontario+Erie+probable low-water phase; (13) lakes Ontario+Erie+Nipissing; (14) lakes Ontario+Erie+Huron+Michigan+Superior. During Phase 14 the margin of the ice sheet stood at about the present height of land south of Hudson Bay. It was flanked by two enormous glacial lakes, Lake Ojibway-Barlow, occupying the site of the present Clay Belt of Ontario, and Lake Agassiz, extending from northern Minnesota over most of Manitoba and extensive areas of Saskatchewan. The development of these northern bodies of water is not fully worked out, and no continuation beyond Phase 14 is therefore possible at the present time. The gradual freeing of the isostatically depressed St. Lawrence Basin led to its flooding by marine waters.

Lougee (1953) presents an interpretation of eastern deglaciation, which he correlates with mid-western lake stages by tracing hinge lines and water-planes of successive phases of isostatic recovery. Recession in the New York-New England area began while the Great Lakes area was still covered with ice, and by the beginning of Phase 1 had proceeded as far as Hartford, Conn. During phases 1 to 4 the New England ice sheet retreated as far as Woodsville, N.H., and the De Geer marine stage in Massachusetts reached its height. From phases 5 to 7 the ice retreated from Schuylerville, N.Y. to Middlebury, Vt., and the De Geer Sea retreated to beyond the present coast line. Phases 8 to 10 correlate with the retreat of ice from the St. Lawrence Valley and formation there of the 700-feet-deep Champlain Sea. The Champlain Sea regressed during Phase 11, and was succeeded by the Ottawa Sea in Phase 12 or 13 (Flint makes the Ottawa Sea contemporary with Phase 11). Phase 14 represents the emergence of the Ottawa Valley and the isolation of Lake Champlain, followed by the Micmac marine stage farther to the east. Lougee's analysis is of particular interest because he takes into account eustatic as well as isostatic sea level changes. He shows that even a modest allowance for eustatic lowering requires the presence of an emergent unglaciated strip along the Atlantic coast as far as Nova Scotia and, in the light of Flint's (1940) studies of isobases, presumably continued on the Grand Banks.

Until recently it was assumed by most students that the Wisconsin was the equivalent of the European Würm, but radiocarbon studies have now cast doubt on this hypothesis (Suess, 1956; Emiliani, 1956). Suess would put the Tazewell at 17,000 to 18,000 years ago, Cary at 13,500 to 14,000, Mankato at 10,000 to

11,000, Cochrane at 6,500 to 7,500, and post-altithermal advance doubtfully at 3,000. This would make Mankato equivalent to European Younger Dryas, Two Creeks equivalent to Alleröd, and Cary equivalent to Older Dryas. According to Suess all stages from Tazewell on are younger than the radiocarbon date of the Younger Loess II of Würm Interstadial 2/3; earlier stages are all beyond the range of the radiocarbon method.

Pollen analysis in America is not as far advanced as in Europe, and there are uncertainties in the correlation with geological stages. Deevey gives the following postglacial chronology: A (immediately following deglaciation), cool, with spruce-fir in most localities; B, warmer, dry, with pine in most localities; C_1, warmer than present, oak-hemlock or oak-beech forest; C_2, warm, dry, oak maximum in the east; C_3, cooler, moister, leading to establishment of present conditions. The A-zone has in some profiles a spruce maximum possibly equivalent to Mankato; the similarity of these profiles to the European postglacial profiles with an Alleröd oscillation (see, for example, von Post, 1946) is striking. Profiles from farther north begin correspondingly later. Series from Quebec are interpreted as showing a brief warm period with *Pinus banksiana*, *Betula papyrifera* and *Quercus* sp., followed by a cooler period with *Picea glauca*, then a warmer period with first a *Pinus banksiana*, then a *P. strobus* + *resinosa*, peak, and finally a recurrence to present conditions with *Picea* spp. abundant and *Pinus* spp. scarce (Potzger, 1953; Potzger and Courtemanche, 1954). This curve, too, is similar to the full European postglacial series, but here there is no doubt that the elapsed time of formation was much shorter.

Some northern and western pollen profiles are now being studied. Hansen (1949, 1949a, 1952) has studied pollen spectra in Alberta. Northern Alberta diagrams show a maximum of *Picea*, preceded and followed by *Pinus maxima*; these sequences are probably young and are inconclusive because of species similarities. However, they are in harmony with the hypothesis of early immigration from a Cordilleran refuge. In the Edmonton region there is evidence of a postglacial xerothermic phase with incursion of prairie species. Hansen (1947) describes profiles in the Pacific Northwest of the U.S.A. He finds evidence of a warm, dry postglacial phase, preceded and followed by cooler conditions.

Heusser (1955) gives profiles from the Queen Charlotte Islands. The base of these is considered to be subsequent to the postglacial marine transgression, but they are older than the oldest profiles studied elsewhere on the British Columbia or Alaska coast. They show an initial tree flora of *Pinus contorta*, *Picea sitchensis* and *Tsuga heterophylla*, followed by a *Pinus contorta* maximum, then by a decline in that species and increase of *Picea sitchensis* and *Tsuga heterophylla*. Heusser considers that a climax forest of modern type was present before the *Pinus ponderosa* invasion, and that this was present throughout the last glaciation.

The whole question of refugia is highly controversial. The nunatak theory of Fernald (1924, 1925) postulated the survival of a large number of species, either endemic or of Cordilleran affinities, in supposedly unglaciated localities in the Gulf of St. Lawrence region. This theory was attacked on strong biological grounds by Wynne-Edwards (1937) and Scoggan (1950). Geological research has shown that almost every refugium postulated by Fernald was heavily glaciated, postglacially submerged, or both (MacClintock and Twenhofel, 1940; Flint, Demorest and Washburn, 1942; Odell, 1938). The strong localization of the species is probably best attributed, as suggested by Wynne-Edwards, to edaphic factors. This solves the problem of the montane relicts, which can be interpreted

as a special facies of the general northward-migrating biota; it does not, however, account for the general occurrence of endemics and disjuncts in the Gulf region, at low levels as well as at high, both as localized forms and as radiants in Labrador and elsewhere in the Northeast. An eastern refugium separate from the general southern glacial-margin strip is required. Data presented by Flint (1940) suggest that isostatic depression probably did not seriously affect the Grand Banks and Sable Island banks, which may well have been eustatically emergent and have provided a haven for maritime relicts, perhaps of ecologically diversified character.

The existence and extent of a cold zone south of the ice constitute another field of controversy. Some authors, e.g., Braun (1950) and Potzger (1946), minimize the importance of the cold zone. Others, such as Dillon (1956), postulate the existence of continuous tundra and taiga zones across the continent to the south of the glaciated area. In support of the first view are (1) absence of tundra pollen from most North American spectra, in contrast to its great prominence in western Europe; (2) the rich and apparently undisturbed nature of the deciduous forests immediately to the south of the glaciated area, as contrasted with their poor and immature appearance on adjacent glacial deposits (Braun, 1950); and (3) the marked differentiation of the arctic and alpine tundra biotas, which would presumably have been in contact on the tundra-belt hypothesis. In support of the second are: (1) the most likely interpretation of weather processes adjacent to an ice-sheet; (2) the presence of definite tundra fossils in the north-central U.S.A.; e.g., *Ovibos moschatus* (Zimmermann)—as opposed to extinct species of *Ovibos*, which may well have had different habitat requirements; (3) the presence of tundra pollen in a few localities (Deevey, 1948); (4) evidence from a variety of sources for a general lowering of temperature levels in glacial stages; and (5) the existence of arctic relicts in various localities in the east and mid-west, e.g., *Dryas integrifolia* at Thunder Bay, Lake Superior (Porsild, 1947).

Glaciation was local in the Cordillera south of the Canada-U.S.A. border, and alpine habitats probably existed there much as they do today, though they were undoubtedly greater in extent and continuity. In British Columbia glaciation is thought to have been general and to have covered Vancouver Island as well as the mainland. Flint shows the Queen Charlotte Islands as having been completely glaciated, but many authors believe they were not.

The most important and least disputed of the northern refuges is Beringia, the extensive unglaciated region on both sides of the Bering Strait. This included the north and west coasts and central valley of Alaska, a large area in eastern Asia, and without doubt a very extensive eustatically emergent area in the Bering Sea bed. The wide closure of the Bering Strait no doubt made for a pronounced climatic difference between North and South Beringia. Evidence for this refugium is very strong, and includes geology, pollen analysis and modern distributions. The last have been discussed extensively in various publications by Hultén and by Porsild.

There is considerable evidence of the existence of one or more refugia that sheltered a small and highly resistant biota in the far north. This would account for the limited ranges of certain central arctic endemics or centrants. Porsild would place this refugium in the northern and western parts of the Archipelago. However, recent observations suggest heavy glaciation at least in the north (Hattersley-Smith, 1955). The very great emergence in recent times in all parts of the Archipelago is strongly suggestive of isostatic recovery after the melting

of a heavy ice load; in any event the submergence, however caused, must have covered a large part of the western islands. It is possible, therefore, that some alternative derivation will have to be sought for this high-arctic biotic element.

Postglacial immigration from the Old World, mainly through Alaska, and to a much lesser extent through Greenland, has had an important influence on the fauna, and the process has been reciprocated by the same route.

VII. Fauna

Vertebrates

Vertebrates are important to insects in five main ways: as predators, as hosts, as sources of carrion, as means of transport, and as reservoirs of disease. No general discussion of the vertebrate fauna can be undertaken here. The subject is thoroughly dealt with in standard works, a selection of which are listed in the bibliography. Among the more important predatory species and groups are:— Mammals: *Didelphis virginiana* Kerr (opossum); Insectivora (moles and shrews); Chiroptera (bats); *Procyon lotor* (L.) (raccoon); *Ursus americanus* Pallas (black bear); Mustelidae, especially Mephitinae (skunks); some rodents. Birds: Limicolae (shore birds); Raptores, especially the sparrow hawk, *Falco sparverius* L., and some of the smaller owls; *Coccyzus* spp. (cuckoos); Picidae (woodpeckers); Caprimulgidae (nighthawk, whip-poor-will, etc.); Micropodidae (swifts); Tyrannidae (flycatchers); Corvidae (crows and jays); Icteridae (orioles, grackles, etc.); Tanagridae (tanagers); Hirundinidae (swallows); Laniidae (shrikes); Vireonidae (vireos); Compsothlypidae (wood warblers—a very numerous and important family); Mimidae (thrashers, etc.); Troglodytidae (wrens); *Certhius familiaris* L. (brown creeper); Sittidae (nuthatches); Paridae (chickadees); Sylviidae (kinglets); Turdidae (thrushes, American robin, bluebirds). Amphibians: numerous species, especially adult Anura. Fish: Coregonidae (whitefish and ciscoes); Salmonidae (salmon and trout); Centrarchidae (bass and sunfishes); Percidae (perch and pike-perch); Lepidosteidae (gar-pike); certain Cyprinidae, etc.

Arthropod parasites of birds and mammals are well represented. Siphonaptera, Mallophaga and Anoplura are numerous and varied. Several species of Cimicidae attack man, bats and swallows. Oestridae, Gasterophilidae and Cuterebridae are numerous. The unusual coleopterous beaver parasite, *Platypsylla castoris* Rits. is a characteristic Canadian species. Larvae of *Protocalliphora* spp. attack birds in their nests. Among Arachnida, Ixodidae, especially the genera *Ixodes* and *Dermacentor*, are numerous; Argasidae occur in the west. A number of regularly or facultatively parasitic mites occur.

Blood-sucking Diptera, especially Culicidae, Simuliidae and Tabanidae, occur in large numbers, the greatest densities being found in the subarctic. The most important mosquito genus is *Aedes*, with species of temporary pools predominating. Several species of *Anopheles* occur, including the good malaria vectors *A. quadrimaculatus* Say and *A. freeborni* Aitken (Twinn, 1945). Simuliidae are serious and even dangerous pests where suitable breeding-sites occur.

Arthropod-borne diseases are less important than in warmer countries, but nonetheless pose a serious problem. Mosquito- and mite-borne encephalitides of man and animals are common, especially on the prairies (Rempel, 1953); sylvatic plague is widespread in Alberta (Brown, 1944); tularemia and Rocky Mountain spotted fever (tick-borne typhus) are of sporadic occurrence. Tick paralysis is locally important in British Columbia (Gregson, 1956). A considerable number of helminth parasites, including Trematoda, Cestoda and Nematoda, have insects as intermediate hosts.

Carrion-feeding and dung-feeding insects are numerous. Calliphoridae are abundant, nowhere more so than in the subarctic. Sarcophagidae, and *Musca domestica* L. and other coprophagous flies are ubiquitous in temperate regions. Among the more prominent saprophagous beetles are Silphidae, especially *Silpha* spp. and *Nicrophorus* spp., and Dermestidae. There are many coprophagous forms, among which Scarabaeidae and Histeridae are especially prominent.

Invertebrates other than Insects

Many of the other invertebrates have no direct relationships with insects. Mollusca, both terrestrial and aquatic, are numerous in Canada, and their zoogeography is of great interest, but space does not permit their discussion here. There is a good representation of Annelida. Some leeches are predatory on small aquatic insects; earthworms are hosts of the larvae of the cluster fly, *Pollenia rudis* (Fallén). True nematodes, mermithids and gordians are frequent parasites of insects, as are many species of Protozoa. Fresh-water Crustacea and other small animals are important as food for aquatic insects. Terrestrial arthropods and all insects and Arachnida will be considered as a unit, of which insects form the overwhelmingly dominant fraction.

Ranges of Insects, Arachnids and other Terrestrial Arthropods

As would be expected from the climatic, vegetational and present and past geographic relations already described, Canada has a balanced, moderately rich, and regionally rather varied fauna. Because of the recent emergence from glaciation—less than 10,000 years for most of the country—the fauna is juvenile and poor in endemics except for arctic and subarctic forms. There is a minor centre of endemism for insects, though an important one for plants, in the Gulf of St. Lawrence region, other minor centres in Vancouver Island and the Queen Charlotte Islands on the west coast. The important Beringian centre sends numerous radiants into Canadian territory, and there are rather vaguely defined centres in the arctic. The arctic region as a whole is characterized by a very high degree of endemism, but of course many of the taxa extend into the Old World and into various parts of the alpine region. Cave faunas are so far as known poor and without endemics such as are found south of the glaciated area. Fresh-water faunas are rich in species but again lack the striking endemism of unglaciated areas. Relicts of the glacial retreat are numerous in bogs and elevated regions, but the period of isolation has in general been too short for any very striking geographic differentiation.

Taxonomic and geographic information is adequate for very few groups of Canadian insects, and even for these statistical tabulations of the geographic data are not yet available. However, it is possible to list a number of characteristic range types, repeatedly found in different taxa. In the present state of knowledge the list cannot be considered exhaustive. The range types depend partly on habitats, reflected in the vegetational regions, and partly on historical factors, determined by glacial refugia and postglacial recolonization. The range types fall into natural groups reflecting community of ecology or history.

First Group: Eastern Ranges

These are ranges related to the deciduous forest formation. The subdivisions are chiefly latitudinal. The highly characteristic southern members of the group do not enter Canada and will not be discussed.

Type E1

Ranges entering Canada only along the north shore of Lake Erie (Fig. 50), i.e., limited by the northern margin of the beech-maple forest region. This very

common type can be subdivided according to the southward configuration of the ranges, but such subdivision has little importance from the Canadian standpoint. Examples: *Phlegethontius sextus* (Joh.) (Lepidoptera); *Argia apicalis* (Say) (Odonata); *Agrilus celti* Knull, *A. subcinctus* Gory, *A. lecontei* Saund. (Coleoptera); *Xylota bicolor* Loew, *Mydas clavatus* (Dru.) (Diptera); *Vespula squamosa* (Dru.) and *Pepsis elegans* Lep. (Hymenoptera). A subtype has a northwestward extension into southern Manitoba. Example: *Epicauta flavocinerea* Blatch.

Type E2

Ranges extending through southern Ontario and a variable distance down the St. Lawrence Valley, extending westward south of the lakes, often as far as southern Manitoba; absent from the Maritime Provinces (Fig. 51). Examples: *Dolba hylaeus* (Dru.) (Lepidoptera); *Orchopeas howardii* (Baker) (Siphonaptera); *Enallagma geminatum* Kellicott (Odonata); *Calligrapha ostryae* Brown, *Chrysochus auratus* (F.), *Silpha americana* L., *Trox variolatus* Mels., *Dichelonyx linearis* Gyll. (Coleoptera); possibly *Spilomyia hamifera* Loew and *S. longicornis* Loew (Diptera); *Vespula vidua* Sauss. (Hymenoptera).

Type E3

Similar to type E2 but entering well into the Maritime Provinces (Fig. 52). A numerous type. Subdivision is possible according to extent of entry into the Maritimes and according to ecological correlation. Examples: *Malacosoma americanum* (F.) (Lepidoptera); *Dichelonyx albicollis* (Burm.), *D. subvittata* (Lec.), *Calligrapha bidenticola* Brown (Coleoptera); *Argia moesta* (Hagen) (Odonata); *Stenoponia americana* (Baker) (Siphonaptera); *Vespula vulgaris maculifrons* (Buyss.), *Smicroplectrus annulipes* Cress. (Hymenoptera); and *Cordilura angustifrons* Loew (Diptera).

Type E4

Southern ranges entering Canada only in the Maritime Provinces or extending much farther north there than elsewhere (Fig. 53). This is a restricted type, but it includes at least three subtypes:—(a) Species associated with salt-marsh or other coastal vegetation. Examples: *Ommatostola lintneri* Grote (Lepidoptera); *Aedes cantator* (Coq.) (see Twinn, 1953), *Ceratinostoma ostiorum* (Curt.) (perhaps an introduced species) (Diptera); *Cleonus calandroides* Rand., *Dichelonyx elongatula* (Schon.) and *Ceutorhynchus hamiltoni* Dietz (Coleoptera). (b) Species not associated with coastal vegetation but able to penetrate far northward in an oceanic climate. Example: *Antepione thisoaria* (Gn.) (Lepidoptera). (c) Migratory species following the coastal route. Example: *Pholus fasciatus* (Sulz.) (Lepidoptera).

Type E5

Ranges largely confined to the white-pine-hemlock-northern hardwoods region (Fig. 55). An extremely restricted type. Examples: *Hemaris gracilis* G. & R. (Lepidoptera); *Exenterus hullensis* Prov., *Neodiprion* spp. (Hymenoptera); *Agriotes fuscus* (Lec.) (Coleoptera).

Second Group: Northeastern Ranges

This group differs from the first in being related not to an ecological formation but to a dispersal area. It is equivalent to the Fernald group of endemic plants, but the insects are mostly less localized than the plants. The geological evidence of glaciation of all formerly postulated plant refugia shows that these are not unaltered relict ranges but that they are the result of dispersal from a glacial or early post-glacial area of isolation, probably on the emergent continental shelf. So far, this group of ranges has been recognized mainly in Lepidoptera among insects. There are two main types.

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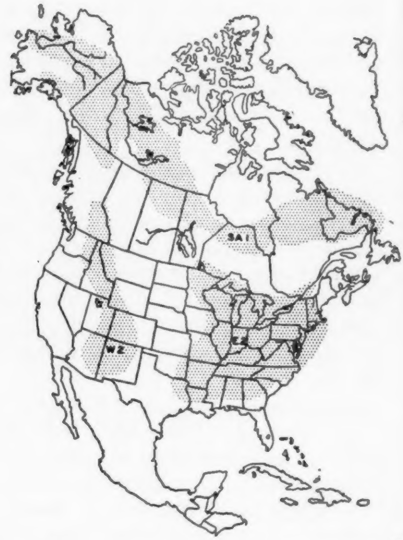

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Figs. 50-53. Typical ranges of Canadian insects. Descriptions of types in text.

Type NE1

Ranges peripheral to the Gulf of St. Lawrence and St. Lawrence estuary (Fig. 50). This type is represented by a few species and by a large number of subspecies. Two subtypes may tentatively be distinguished:– (a) Segregates, often with changed ecology, of widespread temperate taxa. Example: *Papilio brevicauda* Saund. (Lepidoptera). (b) Segregates of boreal taxa. Examples: *Colias interior laurentina* Scud. (Lepidoptera); *Cicindela longilabris novaterrae* Leng, *Phratora purpurea novaeterrae* Brown, and *Sphaeroderus nitidicollis nitidicollis* (Chev.) (Coleoptera), the last two confined to Newfoundland.

Type NE2

Subarctic ranges in Labrador, not extending westward beyond northern Manitoba, commonly with relict isolates on the White Mts., Mt. Katahdin, and the Shickshock Mts. (Fig. 54). A small but clearly defined type. The position of the relicts makes the origin obvious. Examples: *Euxoa dissona* Msch. (Lepidoptera); *Tabanus hearlei* Philip and *T. aequetinctus* Becker, and several Simuliidae (Diptera); *Trechus chalybaeus crassiscapus* Lindr. (Coleoptera-transitional to Type NE1).

Third Group: Central Ranges

This comprises ranges associated with the grassland formation. It is a large and characteristic group.

Type C1

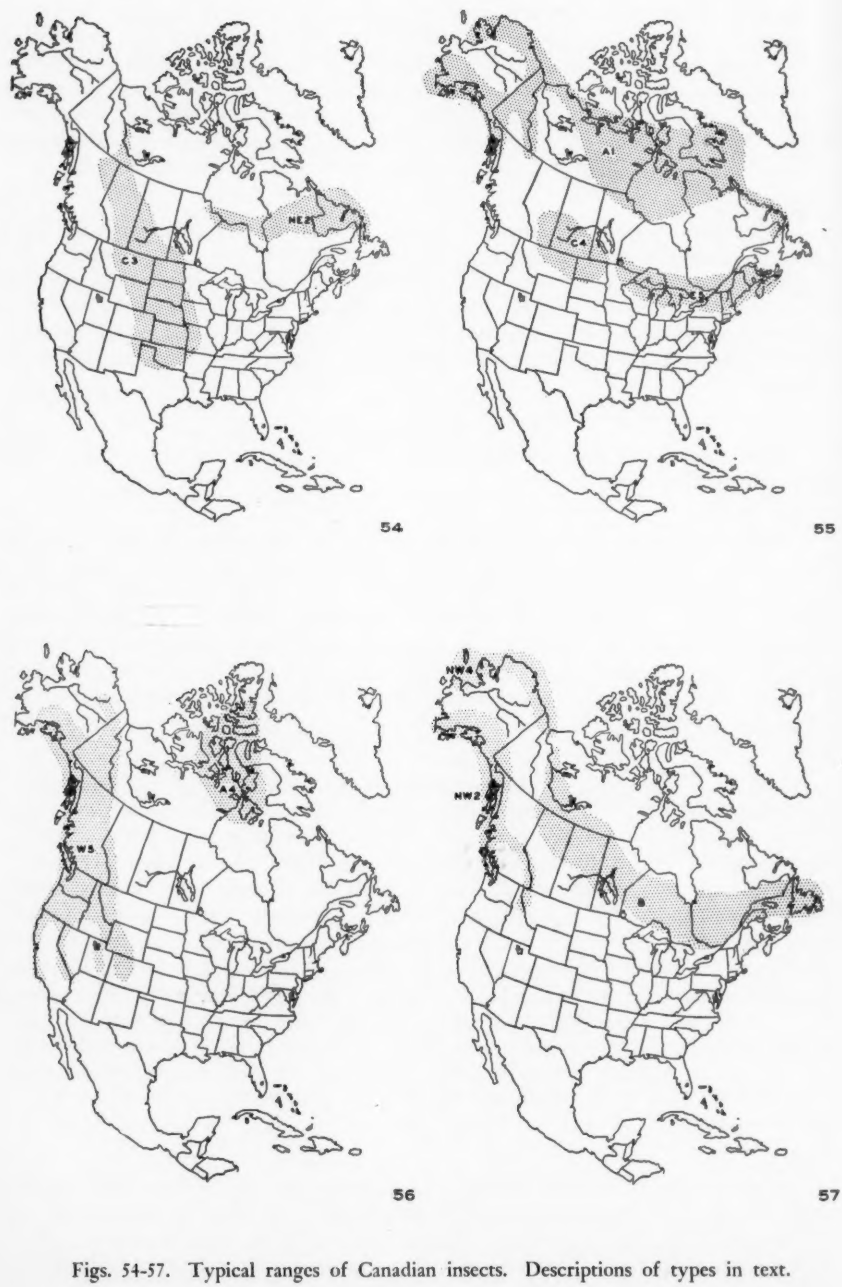
Southern grassland or subdesert ranges entering the Palouse grassland region of southern British Columbia (Fig. 50). The southern part of the range may extend into California, the Great Basin, or both. Examples: *Pseudohazis washingtonensis* Medl. (Lepidoptera); *Thrassis acamantis* (Roths.) (Siphonaptera); *Apiocera haruspex* O.S., *Neomydas pantherinus* (Gerst.), *Anopheles freeborni* Ait. (Diptera); *Ixodes marmotae* C. & K. (Acarina); *Hoplia deserticola* Boyer, *Ctenicera pruinina* Horn (Coleoptera); and *Chirodamnus pyrrhomelas* (Wlk.) (Hymenoptera).

Type C2

Ranges of the Great Plains, barely entering the southern part of the Prairie Provinces (Fig. 53). This is probably a composite type. Three main subtypes can be recognized:–(a) Broad ranges, entering Canada all along the southern borders of the Prairie Provinces. Example: *Cordilura passiva* Curr. (Diptera). (b) Western prairie ranges, entering Canada in Alberta and Saskatchewan. Examples: *Cylindrifrons succandidalis* (Hulst) (Lepidoptera); *Polyphylla decimlineata* Say (Coleoptera); *Loxocera fumipennis* Coq. (Diptera); and *Odontopsyllus dentatus* (Baker) (Siphonaptera). (c) Eastern prairie ranges, some of them confined to the true prairie region, entering Canada in Manitoba. Examples: *Phyllophaga lanceolata* (Say), *Polyphylla hammondi* Lec., *Hoplia laticollis* Lec. (Coleoptera); and *Schinia roseitincta* (Haw.) (Lepidoptera). Several species as yet known only from Criddle's collections near Aweme, Man.–*Pseudotamila awemensis* Dyar, *Titanio criddlealis* Munr., etc.–will perhaps prove to be members of subtype "c".

Type C3

Wide ranges of the Great Plains, extending throughout the Canadian prairies; many of the species range far north of the prairies in suitable habitats, as shown in the map (Fig. 54). Examples: *Colias christina* Edw. (Lepidoptera); *Culex tarsalis* Coq. (Diptera); *Oropsylla rupestris* (Jordan) (Siphonaptera); *Cordilura intermedia* (Curr.), *Sarcophaga cooleyi* Park. (Diptera).



Figs. 54-57. Typical ranges of Canadian insects. Descriptions of types in text.

Type C4

Ranges of the northern Great Plains, largely confined to the prairies of Canada and the northern U.S.A. (Fig. 55). Examples: *Aspilates aberratus* (Hy. Edw.) (Lepidoptera); *Cephus cinctus* Nort. (Hymenoptera); *Dichelonyx kirbyi* Brown (Coleoptera).

Types C2 and C3 commonly combine with C1 to form bipartite ranges. Examples: *Cornifrons simalis* (Grt.) (Lepidoptera), *Neorhynchocephalus sackeni* (Will.), *Copestylum marginatum* (Say) (Diptera).

Fourth Group: Western Ranges

These are ranges of the forested and alpine zones of the Cordillera; the lower zones correspond roughly to the Vancouveran region in the broad sense as mapped by Van Dyke (1940). Although ecologically very different, the altitude zones often have essentially similar geographic relations, and they are conveniently grouped together for the present purpose. Because of the complex topography and multiple zonation, a great deal of subdivision is theoretically possible. Only a few broad range-types will be distinguished here.

Type W1

Southern coastal ranges (Fig. 50). Examples: *Ixodes rugosus* Bish. (Acarina); *Omus* spp. (Coleoptera); *Hydatophylax hesperus* (Banks) (Trichoptera); *Schoenomyza convexifrons* Mall. (Diptera); *Paraptera danbyi* Hlst. (Lepidoptera); *Dolichopsyllus stylosus* Baker (Siphonaptera). A not uncommon subtype has an added section of the range in the Columbia forest region. Examples: *Inocellia longicornis* Albarda (Raphidiodea); *Agriotes sparsus* Lec. (Coleoptera); and *Grotea californicum* Cress. (Hymenoptera).

Type W2

Southern Rocky Mountain ranges, sometimes including neighbouring interior mountains (Fig. 51). Examples: *Stenoporpia excelsaria* (Stkr.) (Lepidoptera); *Peromyscopsylla ravalliensis* (Dunn) (Siphonaptera); *Amphizoa lecontei* Matth., *Hippodamia moesta bowditchi* Johns. (Coleoptera).

Type W3

Southern Cordilleran ranges (Fig. 52). Examples: *Pyrausta versicolor* Warren (Lepidoptera); *Xylota barbata* Loew (Diptera); *Opisodasys keeni* (Baker) (Siphonaptera); *Hippodamia apicalis apicalis* Csy., *Chrysomela aeneicollis* (Schaeff.), *Agriotes ferrugineipennis* (Lec.), and *Chrysobothris monticola* Fall (Coleoptera).

Type W4

Extended coastal ranges (Fig. 53). Examples: *Plectrura spinicauda* Mann., *Opsimus quadrilineatus* (Mann.), and subfamily Trachodinae of Curculionidae (Coleoptera); *Scatophaga frigida* Coq. (Diptera); *Catallagia charlottensis* (Baker), *Dasypsyllus gallinulae perpinnatus* (Baker) (Siphonaptera).

Type W5

Extended Cordilleran ranges (Fig. 56). Examples: *Parnassius smintheus* D. & H. (Lepidoptera); *Megabothris abantis* (Roths.) (Siphonaptera); *Rosalia funebris* Mots. (Coleoptera); and *Bombus flavifrons* Cress. (Hymenoptera).

Fifth Group: Northwestern Ranges

These are ranges apparently related to the unglaciated region of Beringia. Some of the types are distinguishable with difficulty from ranges of adjoining groups, similar ranges being derivable from different points of postglacial origin.

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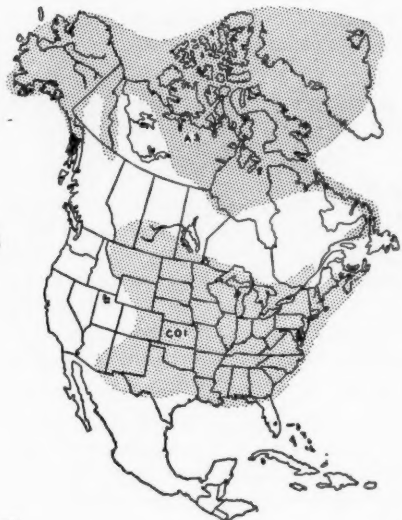

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Figs. 58-61. Typical ranges of Canadian insects. Descriptions of types in text.

Type NW1

Aleutian-southern Alaskan ranges (Fig. 50). This is considered by Hultén to be an important type in plants. In insects it is probably much less so, and in Lepidoptera is mainly exemplified by subspecies. Examples: *Udea itysalis* (Wlk.), unnamed subspecies (Lepidoptera); *Scatophaga crinita* Coq. (Diptera); *Dasypsyllus stejnegeri* (Jord.) (Siphonaptera); *Sthereus ptinoides* (Germ.) (Coleoptera); *Cratichneumon* sp. (Hymenoptera).

Type NW2

Southern Alaska-northern Rocky Mountains ranges (Fig. 57). Like the preceding, this is an important type in plants but much less important in insects. Examples: *Boloria astarte* (Dbl.) (Lepidoptera); *Thrassis spenceri* (Wagn.) (Siphonaptera); *Bombus sitkensis* Nyl. (Hymenoptera).

Type NW3

Alaska-northwestern Canada ranges (Fig. 58). These may be arctic, subarctic or boreal. There are many ranges of this type. Examples: *Boloria pales* (Schiff.) (Lepidoptera), *Megabothris calcarifer gregsoni* Holl., *Malaraeus penicilliger dissimilis* Jord. (Siphonaptera); *Carabus truncaticollis* Esch., *C. vietinghoffii* Adams (see Hicks, 1953), *Phratora interstitialis* Mann. (Coleoptera); *Bombus strenuus* Cress. (Hymenoptera).

Type NW4

Coastal ranges in western and northern Alaska and northwestern Canada (Fig. 57). The species of this group include a high proportion of striking and unusual endemics. Examples: *Barrovia fasciata* Skin., *Diasemia alaskalis* Gibs., *Crymodes murrayi* (Gibs.) (Lepidoptera); *Chrysolina subsulcata* (Mann.), *Pterostichus agonus* Horn (Coleoptera).

Sixth Group: Boreal Ranges

This is a very large class of ranges (Fig. 57). Species of the boreal forest are among the most characteristic insects of Canada. Most of the species range throughout the boreal forest, either in strictly forested habitats or in subsidiary habitats, such as bogs, marshes or burn sequences. The range usually extends farther north and west than is shown in the figure. No subdivision of the type seems possible at present. Examples: *Choristoneura pinus* Free. (Lepidoptera); *Xylota bigelowi* (Curr.) (Diptera); *Amara* (*Curtonotus*) *hyperborea* Dej.; *Cicindela longilabris longilabris* Say + *C. l. novaterrae* Leng (Coleoptera).

Seventh Group: Subarctic Ranges

Purely subarctic species are few. One special class has already been considered as type NE2, above. Two additional types are recognizable.

Type SA1

General subarctic ranges (Fig. 51). These occasionally straggle a short way into the arctic region on the one hand and the boreal on the other. Examples: *Sympistis melaleuca* (Thnbg.) (Lepidoptera); *Sericomyia sexfasciata* (Wlk.) (Diptera); *Vespula albida* (Slad.), *V. intermedia* (Buyss.) (Hymenoptera).

Type SA2

Western subarctic ranges (Fig. 52), occupying all or most of the part of the region that lies west of Hudson Bay. Examples: *Pachnobia morandi* Benj. (Lepidoptera); *Catallagia dacenkoi fulleri* Holl. (Siphonaptera).

Eighth Group: Arctic Ranges

Several of the main types are determined by features of their Old-World or Atlantic ranges. These distinctions, though important, will not be considered here.

Type A1

Broad low-arctic ranges (Fig. 55). This is probably the most numerous type; it includes both Holarctic and strictly North American subtypes. Examples: *Aspilates orciferaria* (Wlk.) (Lepidoptera); *Pleurochaeta simplicipes* (Becker), *Lasiocellus sahlbergi* Becker, *Eupogonomyia pribilofensis* Mall. (Diptera); *Hydroporus polaris* Fall, *Nebria nivalis bifaria* Mann. (Coleoptera); *Bombus sylvicola* var. *johanseni* Sladen (Hymenoptera).

Type A2

Western low-arctic ranges (Fig. 60). This is a restricted variant of type A1 that includes species not found in Ungava and southern Baffin Island. Examples: *Aspilates*, unnamed species (Lepidoptera); *Blethisa catenaria* Br., *Pleurostichus vermiculosus* Men. (Coleoptera). Some species with ranges of this type, though true tundra insects, are restricted to the immediate vicinity of tree-line, and may eventually have to be recognized as a distinct subtype.

Type A3

Comprehensive arctic ranges (Fig. 59). This type includes species widely distributed in all latitudes in the arctic region. Examples: *Boloria polaris* (Bdv.) (Lepidoptera); *Megabothris groenlandicus* (Wahlgren), *Ceratophyllus lunatus tundrensis* Holl. (Siphonaptera); *Aedes nigripes* Zett., *Limnophora* (*Spilogona*) *latilamina* Collin, and *Scatophaga apicalis* Curt. (Diptera).

Type A4

Central arctic endemics (Fig. 56). A small but distinctive group of species inhabits ranges of various sizes in the central arctic. Examples: *Lycaena feildeni* (McL.), *Colias boothii* Curt. (Lepidoptera).

Type A5

High arctic endemics (Fig. 58). This comprises a very few species primarily at home in the high arctic. Examples: *Byrdia groenlandica* Hom. (Lepidoptera), *Exorista*, undescribed species (Hymenoptera).

Ninth Group: Combined Ranges

Individual taxa may of course occupy almost any combination of adjacent range types. No attempt can be made to list all of these. Some of the types defined above can be considered as combinations of more restricted types. Three of the more important additional combinations are listed here.

Type CO1

Eastern and central ranges (Fig. 59). These are associated with open habitats or xeric vegetation in the east and are at home in similar habitats on the interior plains, giving them more or less continuous ranges east of the Rockies. Examples: *Hyalophora cecropia* (L.) (Lepidoptera); *Ctenophthalmus pseudagyrtes* Baker (Siphonaptera); *Epicauta fabricii* (Lec.) (Coleoptera).

Type CO2

Boreal and western ranges (Fig. 60). These are ranges that extend widely through the northern and western coniferous forests. Examples: *Caripeta divisaria* Wlk. (Lepidoptera); *Cicindela longilabris* Say (excluding some prairie forms of doubtful conspecificity), *Chrysobothris trinervia* (Kby.) (Coleoptera); *Pegomyia univittata* (von Roser) (Diptera).

Type CO3

Arctic and western ranges (Fig. 61). These are the familiar arctic-alpine ranges. Examples: *Dasyuris polata* (Dup.) (Lepidoptera); *Amara* (*Curtonotus*) *alpina brunneipennis* Dej. (Coleoptera); *Okeniella caudata* (Zett.), *Aedes impiger* (Wlk.) (Diptera); *Bombus balteatus* Dahlb. (Hymenoptera).

Tenth Group: Ranges of Introduced Species

Ranges of introduced species do not follow any simple geographic pattern or rule of behaviour. Some introductions have spread throughout the temperate parts of the country, e.g., *Pieris rapae* (L.), others are spreading but have not reached their full extension, e.g., *Thera juniperata* (L.). Still others are spreading slowly, e.g., *Stilpnotia salicis* (L.), and others have remained in the region of introduction, e.g., *Operophtera brumata* (L.) in southern Nova Scotia, or even on very restricted sites, e.g., *Agriotes lineatus* (L.) in the neighbourhoods of four ports in the Maritime Provinces. Many introduced species are associated with crops, weeds or disturbed sites, but, as already noted, a considerable number have succeeded in breaking into climax associations, where they have sometimes caused severe upsets. Brown (1940, 1950) gives ranges of a number of introduced Coleoptera. Ranges of introduced pests of crops and forests are followed in the voluminous literature of economic entomology.

Faunal Divisions and Their Insects

No critical or historical survey of the faunal divisions proposed for the Nearctic region can be undertaken here. The reader is referred to Daubenmire (1938) and Kendleigh (1954). The faunal divisions of Canada are, as might be expected, closely related to the vegetational regions. For several reasons, however, the vegetational classification cannot be adopted unchanged for entomological purposes. Perhaps the most important of these reasons is ignorance. Entomology has lagged far behind botany in the geographic and ecological study of species. In the majority of groups species taxonomy has hardly begun to be worked out, collecting is in its infancy, and classification of the material when collected is either impossible or cannot be done with sufficient accuracy and rapidity for zoogeographic purposes. Even in well-known groups the emphasis has been on taxonomic rather than on geographic collections, and we have abundant knowledge of the species of restricted areas, rather than evenly distributed knowledge of the country as a whole. The knowledge that exists is scattered and unco-ordinated. Until a number of groups have been studied on a geographic basis only the broad outlines of a faunistic treatment can be given, and correlation with the finer divisions of the vegetation structure will be impossible except in specific cases.

Other reasons depend on the insects themselves. Insects are more mobile than plants, and tend to disperse faster from refugia and to range farther from their nuclear habitats. The relationship of insects to plants is often rather general. Many species, it is true, are dependent on a single plant species as a host, but many others will eat various species of a genus or family, and a large number are highly polyphagous. The ranges of such species can extend beyond those of single plant species. The ranges of predators and parasites are often even wider than those of their phytophagous hosts, and broad ranges are the rule in insectivorous groups. Insects are not directly affected by edaphic factors to the extent that plants are, and they can escape by voluntary movement from a range of climatic conditions that the sessile plant must endure on the spot.

All these factors combine to make insect faunal zones appear broader and less sharply defined than the zones of the vegetation. Nonetheless, certain units are immediately obvious, others appear with closer study. In the east the classical Merriam life-zone system is satisfactory, with changes of detail to accord with modern knowledge, and with subdivision to fit local historical and environmental effects. In the west a more complicated system is required to accommodate the distribution-patterns adequately, but such a system is hard to achieve in the

present state of knowledge. I recognize the following main divisions: Carolinian, Alleghenian-Acadian, Canadian, Hudsonian, arctic, alpine, Cordilleran forest, and interior grassland. In the general world classification these would rank as provinces of the Holarctic (or if preferred the Nearctic) region. Grouping of the provinces in subregions depends largely on faunas extralimital to Canada, and is not attempted here.

Carolinian Province

The Carolinian province (=eastern division of upper austral zone) is coextensive with beech-maple forest region (=deciduous forest region of Halliday) and is confined in Canada to the part of Ontario immediately north of Lake Erie. It has a rich temperate fauna, comparable to those of the Chicago or New York City areas. A very large number of species occur here that do not range farther north in Canada; examples have been cited under range type E1, above.

Others, of types E2, E3 and some combined types, range to the north and often to the west, beyond this zone, e.g.: *Papilio glaucus* L., *Antheraea polyphemus* (Cr.), *Catocala unijuga* Wlk. (Lepidoptera). Northern species are poorly represented, except in bogs; *Picea glauca* is absent, and with it a number of associated insects. One of the characteristic features of this region and the next is the presence of species with close relatives in the far-removed temperate forests of eastern Asia. A few examples are:

	North America	Asia
Lepidoptera	*Sphecodina abbotti* (Swains.)	*S. caudata* Br. & Gr.
	Catocala cerogama Gn.	*C. lara* Brem.
Trichoptera	*Eubasilissa pardalis* (Wlk.)	*E. regina* (McL.)

Parallels in plant and vertebrate distributions are well known, and this type of range is attributed to fragmentation of the earlier Holarctic temperate-forest biota in late-Tertiary and Pleistocene time (Reinig, 1937). These are really attenuations of the tripartite ranges in which a third member of the series is found in the forested zone of Europe, e.g.: *Amphipyra pyramidea* (L.), Europe, *A. monolitha* Gn., Asia, and *A. pyramidoides* Gn., North America. The bog fauna of this region is in general like that of the next, though bogs are fewer and more restricted and the fauna tends to be reduced.

No subdivision of the province is necessary in Canada.

Alleghenian-Acadian Province

The Alleghenian-Acadian province (=eastern division of transition zone) is nearly coextensive with the hemlock-white pine-northern hardwoods forest region, but excludes some boreal areas, mainly in Gaspé and the Maritime Provinces, that are placed in that region on the forest map (Fig. 26). The fauna of the Alleghenian-Acadian province is a mixture of northern and southern elements, with the latter predominating. Many species reach their northern or southern limits here. There is a small admixture of endemic taxa, but they are not a conspicuous part of the fauna. Examples of southern species reaching their northern limit in this province are: *Papilio polyxenes* F., *Pieris virginiensis* Edw., *Lethe eurydice* (Joh.), *Actias luna* (L.), (Lepidoptera); *Astenophylax argus* Harr. (Trichoptera); *Corydalis cornuta* L. (Megaloptera). Examples of northern species reaching their southern limit (in eastern North America) here are: *Smerinthus cerisyi* Kby., *Pachysphinx modesta* (Harr.), *Syngrapha rectangula* (Kby.) (Lepidoptera). Examples of species endemic or nearly endemic in this region are: *Hemaris gracilis* (G. & R.), *Sphinx canadensis* Bdv., *Sthenopis thule* (Stkr.) (Lepidoptera); and *Banksiola concatenata* (Wlk.) (Trichoptera). The

high proportion of disturbed or cultivated land has permitted a great increase in the ranges and abundance of open-country species in this province as in the last. There are many introduced European species, among which can be mentioned *Operophtera brumata* L., and *Thera juniperata* L. (Lepidoptera); and *Carabus nemoralis* Mull. (Coleoptera). Bogs are widespread. They have a characteristic fauna, consisting largely of species of the Canadian province, with a few Hudsonian species and Alleghenian endemics added. Among some of the many characteristic species of bogs are: *Incisalia lanoraiensis* Shep., *Oeneis jutta* (Hbn.), *Eufidonia discospilata* (Wlk.), *Isturgia truncataria* (Wlk.), *Exyra rolandiana* Grt. (Lepidoptera); *Chlamisus chamaedaphnis* Brown, *Sericus brunneus* (L.) (Coleoptera). Many of these species farther north are not confined to bogs, but have a general distribution. Some species seem to be restricted to bogs by the occurrence of their food plants, others by local climate or other factors of the physical environment.

Although the insects of this faunal province are better known than those of any other part of Canada, the collections have come mainly from a few restricted areas, and there has as yet been no serious comparative study even of these. Geographic subdivision must therefore be tentative. There are three main areas: the maritime area, from New Brunswick eastward; the central area, from the lower St. Lawrence valley to Lake Huron, and the western area, from Lake Superior to southeastern Manitoba.

The *maritime area* is characterized by subspecific differentiation of a high proportion of species in groups that tend to have obvious geographic variation, by the absence of many species common in interior areas, by the presence of a few native species and a considerable number of European introductions not found in the interior, and by a general mixing of faunas, with northern and southern species found together, and species found outside the habitats they frequent in inland areas. Ferguson (1954) gives some regional and habitat correlation of Lepidoptera in Nova Scotia, basing them on his extensive field experience in that province, but no general study of the maritime area has so far been made.

The *central area* has several obvious natural divisions. The *southern Ontario plains*, north of the Carolinian zone along Lake Erie, still have a high proportion of infiltrating southern species and forms: *Plebeius* (*Lycaeides*) *melissa samuelis* (Nab.), *Limenitis arthemis* f. *proserpina* Edw., etc. The *lower Ottawa and upper St. Lawrence valleys* have a more purely Alleghenian fauna, with one species after another dropping out to the northeast and northwest. The *southern Canadian shield* lacks some species found on the plains and has some others that seem to be limited by its boundary: *Colias interior* Scud. (found farther south as relict populations in bogs), *Glaucopsyche lygdamis couperi* (Grt.), *Oeneis chryxus strigulosa* McD., and *Coenonympha tullia inornata* Edw. are examples. The Appalachian area of the Eastern Townships and the lower St. Lawrence really are closely similar in their faunas to the southern Canadian shield.

The *western area* is very poorly investigated. The extensive collection of Lepidoptera made at Hymers, Ont., many years ago contains a high proportion of bog species, but among the more eurytopic elements a number of eastern species are present: *Palpita arsaltealis* (Wlk.), *Munroessa serralinealis* (B. & B.), etc. *Platytes vobisne* Dyar has been recorded from Canada only in this area.

The aquatic fauna of this province is very rich. The St. Lawrence and other large rivers produce massive quantities of Trichoptera, Ephemerida and Chironomidae. Over 80 species of larger Trichoptera occur commonly at

light in the vicinity of Ste. Anne de Bellevue, P.Q., on the Ottawa River. Hydropsychidae, Leptoceridae, and Psychomyiidae are the dominant families, with individual species of Helicopsychildae, Molannidae, Sericostomatidae and other families numerous. Ephemerida are equally numerous. There are many aquatic Coleoptera representing a larger number of species than occur farther north or in the Lake Erie region.

Canadian Province

This province is characterized by a closed coniferous-forest climax with *Picea glauca, P. mariana* and *Abies balsamea* as dominants. *Picea rubens* is a tree of quite different ecological associations, and communities in which it appears are referable to the Alleghenian-Acadian province. The Canadian province occupies approximately the area shown in solid green on the vegetation map. The insects of the climax coniferous forest, and of its subclimax and aboreal preclimax stages are remarkably well known, thanks to the Forest Insect and Disease Survey[1]. Much of the information is as yet unpublished, but regional accounts of the most destructive tree-feeding species are given in the *Annual Reports* of the survey, and comprehensive reports are in preparation. Among some of the more important conifer-feeding insects are: *Lambdina fiscellaria* (Gn.), *Acleris variana* Fern., *Choristoneura fumiferana* (Clem.), *C. pinus* Free., and *Petrova albicapitana* (Busck) (Lepidoptera); *Pikonema alaskensis* Roh. and *P. dimmocki* (Cress.), *Neodiprion* spp., and *Pristiphora erichsonii* (Htg.) (Hymenoptera); and *Pissodes strobi* (Peck) (Coleoptera). Species of *Populus* and *Betula* are infested by many insects. Important species are: *Malacosoma disstria* Hbn. and *M. pluviale* (Dyar), *Tetralopha* spp., *Meroptera* spp., *Archips conflictana* (Wlk.), *Lithocolletis salicifoliella* Chamb., *Bucculatrix canadensisella* Chamb. (Lepidoptera); *Arge pectoralis* (Leach) (Hymenoptera); and *Gonioctena americana* (Schaeff.) (Coleoptera). There is a very large group of heath, shrub, moss and lichen insects. Many are restricted to bogs farther south, and in turn some Hudsonian insects are restricted to bogs in the Canadian province, e.g., *Boloria eunomia* (Esp.), *B. titania* (Esp.) and *B. freija* (Thun.). Some, like *Oeneis jutta* Hbn., are restricted to bogs in all zones.

Aquatic insects are numerous, especially Simuliidae and *Aedes* spp. (Diptera); Limnephilidae, Hydropsychidae, Molannidae, Sericostomatidae and *Mystacides* spp. (Trichoptera); *Rhithrogena* spp., *Ephemerella* spp., *Hexagenia* spp., etc. (Ephemerida); and a wide variety of Plecoptera and Coleoptera. There are probably fewer species than in the Alleghenian-Acadian province.

On the whole the Canadian province is so homogeneous that little faunistic subdivision is warranted. Halliday's division of the boreal forest into eastern and western parts has been mentioned above. So far as known there is no sharp faunal differentiation corresponding to Halliday's division. Western species often fail to range all the way across the boreal forest; a considerable number, such as *Nemeophila plantaginis* (L.) (Lepidoptera) and *Ctenicera nigricollis* (Bland), *C. morula* (Lec.) and *C. aeripennis aeripennis* (Kby.) (Coleoptera), drop out at various points in northern Ontario. A number of species known formerly only from the west have been found in the past few years ranging well into Eastern Canada: *Plebeius saepiolus* (Bdv.) to Nova Scotia, *Apantesis williamsi* Dodge to New Brunswick (Ferguson, 1954), *Erebia discoidalis* Kby. and *Malacosoma pluviale* (Dyar) to northern Quebec, and *Oeneis macounii* Edw. to eastern Ontario. It is not certain whether these

[1]An activity of the Forest Biology Division, Science Service, Canada Department of Agriculture.

represent actual recent extensions or only the result of more thorough collecting. At present a division into eastern and western areas does not seem justified, though more detailed studies may change the picture in future.

The Gulf of St. Lawrence area poses a special problem. As already mentioned, there is a strong tendency to minor endemism in this area, Canadian-zone endemics of similar facies often being found on both shores of the lower St. Lawrence, in New Brunswick, Nova Scotia, Newfoundland and southern Labrador. The presence of these endemics, mainly subspecific, and the possible absence of a considerable number of species found farther west, makes the recognition of a distinct *Gulf of St. Lawrence area* useful. The fauna of Newfoundland is distinguished mainly by the absence of a very large number of species fôund on the mainland. Examples of missing species are: *Smerinthus cerisyi* Kby., *Pachysphinx modesta* (Harr.), *Sphinx gordius* Cr., to name but a few in one family. Other examples are given by Reeks and Smith (1945). Perhaps in compensation, some species seem abnormally abundant, e.g., *Oligia bridghami* G. & R. There are some endemic subspecies in Newfoundland, but these are mainly only intensifications of general Gulf of St. Lawrence area modifications. Some species are known at present only from Newfoundland (Krogerus, 1954; Hackman, 1954), but these are in poorly known groups, and will very likely be found elsewhere. Lindroth (1955) did not find any endemic species of Carabidae, the several new species he described from Newfoundland being known from other localities as well, but there is a strongly characterized endemic carabid subspecies, *Sphaeroderus nitidicollis nitidicollis* Chevr. Newfoundland populations of many species of Carabidae are abnormally large in average individual size.

Hudsonian Province

The Hudsonian province is the region of .open conifer-lichen climax that lies between the closed Canadian forest and the treeless arctic tundra east of the Mackenzie Delta. It is coextensive with Halliday's northern transition section. The most striking feature of the Hudsonian province as compared with the Canadian is the great impoverishment of its fauna. A large proportion of the Hudsonian fauna is composed of tolerant Canadian-zone species, whose range extends northward. As already noted, there is a well-marked eastern-Hudsonian endemic component in the Hudsonian fauna of Labrador, including *Pachnobia* spp., *Euxoa dissona* Msch., *Aspilates conspersaria* Stgr., and *Xanthorhoe algidata* (Msch.); there are also some Amphiatlantic elements in this Labrador fauna, e.g., *Crymodes maillardi* (Gey.), *Crino sommeri* (Lef.) and *Loxostege ephippialis* (Zett.). The western part of the Hudsonian has its own set of specialties, probably of Beringian or Euro-Siberian derivation: *Papilio machaon* L., *Pachnobia morandi* Benj., etc. Other typically Hudsonian species have transcontinental ranges: *Tabanus metabolus* McD., *Chrysops nigripes* Zett. (according to Freeman, 1953).

Aquatic insects of the Hudsonian region differ considerably from those of the Canadian. Ephemerida are greatly reduced. Trichoptera are represented mainly by Limnephilidae. Simuliidae and *Aedes* spp. are present in enormous numbers and considerable variety of species (Twinn, *et al.*, 1948; Twinn, 1949; Hocking and Pickering, 1954; Hocking and Richards, 1952; Hocking, Richards and Twinn, 1950; Freeman, 1952).

No division other than that into eastern and western areas seems warranted at present.

Arctic Province

The insect fauna of the arctic province differs strikingly from that of the forested zones to the south. The arctic fauna contains a very high proportion of species confined to it (Van Dyke, 1940; Freeman, 1952a), though for the most part they belong to more widely distributed genera. The relationship to the arctic fauna of the Old World is very close, circumpolar species far outnumbering all others. The fauna as a whole is scanty, but some of the species are very abundant. The Diptera are the best-represented order, with Hymenoptera and Lepidoptera moderately well represented and Coleoptera poorly represented. Among characteristic genera of Lepidoptera are *Colias, Boloria, Oeneis, Erebia, Anarta* and *Aspilates*. Trichoptera are represented mainly by Limnephilidae, with the *Radema* group particularly well developed.

Division into areas is tentative at present. A *low-arctic area*, including arctic Labrador and Quebec, the arctic zone of the mainland of the Northwest Territories at least as far north as the base of the Boothia Peninsula and as far west as the Mackenzie delta, has a moderately rich fauna, composed largely of circumpolar species, but with some endemics. With this area can be associated Southampton Island, southern Baffin Island and southern Victoria Island. There is some differentiation between the eastern and western parts of this area, but its importance cannot yet be assessed. The *high-arctic area*, including the Queen Elizabeth Islands and probably some neighbouring areas to the south, is characterized by absence of many species of the low-arctic area, such as *Aspilates orciferaria* (Wlk.) and sharp reduction in the abundance of many others, such as *Dasyuris polata* (Dup.) (Munroe, 1951); on the other hand, a few species, such as *Byrdia groenlandica*, are confined to this region, and others, such as *Psychophora sabinii* (Curtis), reach their greatest abundance in it. The *northwestern coastal plain*, i.e., the coastal plain west of the Mackenzie River, has many species not found farther east, e.g., *Barrovia fasciata* Skin., *Neobarrovia keelei* Gibs. and *Diasemia alaskalis* Gibs. In addition to these elements, most components of the normal arctic fauna occur in this area. The *arctic Cordilleran area*, including the Mackenzie Mountains and all mountains lying to the west of them, is poorly known, but evidently contains Cordilleran elements such as *Oeneis brucei yukonensis* Gibs. and Beringian elements such as *Parnassius eversmanni* Mén. It is very likely that this area is heterogeneous. In particular the St. Elias Mountains may have a distinctive fauna, but our knowledge is insufficient for a definite subdivision.

Alpine Province

Similarities and differences in the alpine and arctic environments have already been noted. The faunas show a corresponding assortment of similar and different features.

Alpine faunas of the Cordillera contain many species that are common on the arctic tundra: *Dasyuris polata, Colias nastes* Bdv. and *Oeneis taygete* Gey. are excellent examples. However, a large number of arctic species are unknown in the Cordillera: *Colias hecla* (Lef.), *Aspilates* spp., *Boloria polaris* (Bdv.), etc. There is instead a series of endemic alpine species, of which some examples have already been mentioned. *Colias meadi* Edw., *Boloria alberta* (Edw.), and *Orenaia trivialis* B. & McD. belong to this type.

During the summer flight season the native fauna of the alpine zone is very heavily contaminated with insects of lower zones that fly or are

blown up the mountain slopes, and field collections usually have a very mixed aspect. The impact this may have on the ecology of the alpine zone has not been fully investigated.

Although alpine insects have been collected at a number of localities in the Canadian Cordillera, the collecting has on the whole been sporadic and much of the material has been dispersed to different collections. No comparison of the faunas of different areas of the alpine province is possible at this time. Dod (1908) and Whitehouse (1918) have published graphic accounts of collecting in the alpine zone of the Rocky Mountains.

Cordilleran Forest Province

We have already seen that the forests of the Cordillera belong to several distinct ecological associations and also that a number of different types of insect ranges enter the region. Unfortunately our knowledge of zonation and ecological correlation in the insect fauna is far from complete. Large areas of British Columbia and the Yukon Territory have not been sampled entomologically, and even the better-collected parts of British Columbia are surprisingly poorly known. Spencer (1952) gives a documented summary of knowledge up to 1951, to which must be added papers by Ross and Spencer (1952) and Schmid and Guppy (1952) on Trichoptera, by Lane (1952) and Clark (1956) on Coleoptera, and by Ross (1955) and Ross and Evans (1955, 1956, 1956a) on Lepidoptera. Locality and often host data are available, but there is seldom any association with altitude zones of ecological communities. Such information is usually lacking from specimens in the major collections, but a wealth of information on forest species has been accumulated in the files of the Forest Insect Survey, and will ultimately be published.

The most obvious division in the insect fauna of the forested zones is between the coastal zone—corresponding in extent to the coast forest region—and the interior. The striking differentiation of the coastal fauna in certain groups is emphasized by Van Dyke (1940), who gives references to earlier literature, and by Linsley (1940), among other authors. Similar differentiation in the flora has been investigated by Hultén (1941-50). Theoretically the interior forest fauna would be expected to show zonal differences corresponding to the forest zones. Though such differences doubtless exist, they cannot be satisfactorily demonstrated with present knowledge, though some individual instances of zonal limitation are known. Ranges of certain species, e.g., *Udea washingtonalis* (Grt.), suggest that primarily coastal taxa may often reappear in the Columbia forest region, but precise ecological correlations are not yet available.

Differences within the Cordilleran fauna must not be permitted to obscure its considerable degree of overall unity. This unity is determined partly by the fact that all the forest regions resemble one another in having coniferous climax dominants and a rather limited range of broad-leaved trees, belonging largely to the same genera, in the preclimax and understory vegetation. Many of the insects are only loosely associated with forest zones, and a substantial element of the fauna is wide-ranging within the Cordillera. A common history ties the faunas of the different zones and ranges together and separates them from the Canadian and Hudsonian provinces with their similar coniferous climax. In some groups, such as Hymenoptera and Lepidoptera, the differences between coastal and interior faunas are much less striking and obvious than in the Coleoptera and Neuroptera, where the classical "Vancouveran" fauna is highly developed. Groups of wide distribution in the Cordillera, and more or less confined

to it at least in the Nearctic region are: *Pseudohazis*, *Parnassius*, *Enypia* (Lepidoptera); Raphidiidae (Raphidiodea); Grylloblattidae (Orthoptera); etc. A number of groups of wider distribution are particularly well developed in the Cordilleran region, often bursting into a rather characteristic type of population-swarm, consisting of weakly differentiated species and more or less strongly differentiated subspecies, interlocking in a confusing pattern. Some examples in Lepidoptera are the genera *Euphydryas*, *Argynnis*, *Udea* and *Evergestis*.

The *coastal area*, as already noted, has an imposing array of endemic species, genera and even families, examples of which have already been given under range types W1, W4 and NW1, above. There is, however, a tendency for taxa otherwise confined to this area to reappear in the Columbia forest of the interior area, e.g., *Udea washingtonalis*, (Lepidoptera); *Inocellia longicornis* Albarda (Raphidiodea). The endemic elements of the fauna are separable in a general way into northern, southern, and widely ranging types, but there is considerable intergradation, and statistical study will be required before the reality of the apparently discrete types can be established. A subdivision based on forest classification, into southern, central and northern coast sections and madrona-oak section will probably prove satisfactory from the standpoint of the fauna, but it will almost certainly be necessary to separate the Queen Charlotte Islands as a fifth section.

The *interior area* lacks many species present in the coastal area, and has some not found on the coast. The area is heterogeneous as to fauna, and will undoubtedly have to be subdivided when better distributional information and ecological correlations are available. Such a subdivision will not be attempted here.

Grassland Province

The grassland province comprises the areas occupied by the grassland formation, viz., the prairies of Manitoba, Saskatchewan and Alberta and the interior grasslands of British Columbia. The natural geographic division of the region is to a considerable extent reflected in the fauna. The Okanagan and other southern British Columbia valleys have many species that do not occur elsewhere in Canada, but they have also many species in common with the prairies. The species not found on the prairies are partly of Californian, partly of Great Basin affinities. Conversely, the prairies have many species not found in British Columbia. Although insects have been collected extensively in both areas, we have regrettably little knowledge of the detailed distribution or composition of the faunas.

In the *British Columbia grassland area* there is known to be a progressive dropping-out of southern and xeric elements upward and towards the north, but there is little information on precise zonal and habitat correlations. Grassland elements go a long way north, though much diluted by woodland species. I have seen lepidopterous species of grassland affinities from as far north as Terrace, B.C. The subarid elements are, however, confined to the southernmost section of the valleys—especially the Okanagan—just north of the United States border. In this zone *Melitara dentata* Grt. *Itame colata* (Grt.) and other primarily Sonoran elements are found. This whole area is being greatly modified by cultivation and grazing, and it is to be hoped that zonal associations will be studied before the natural habitats are altered beyond recognition.

In the *prairie area* our knowledge of the ecological and geographic relationships of insects is likewise rudimentary. Strickland (1938) has erected a zonal system for Alberta, which he and other authors have applied in a series of

distributional lists, but no general analysis of prairie distributions has yet been made; indeed, in most groups it is unlikely that collecting and taxonomy are sufficiently advanced to justify such analysis. Bird (1927) gives a description of insect life in the restricted but extremely varied environment around Aweme and Treesbank, Man. Work now being carried out by Dr. A. R. Brooks can be expected greatly to enhance our knowledge of insect ecology and distribution on the prairies. In conjunction with the rapid development of the science of plant ecology in the area, it is likely that this and other entomological work will rapidly lead to an unrivalled understanding of the prairie environment.

At present only a few generalities can be stated. The fauna of the prairies must tolerate dry, extremely continental conditions. Frequently salt or alkali tolerance is also necessary. The fauna contains a large proportion of grass-associates. Cutworms (*Euxoa* spp. and other Phalaenidae), Crambinae and other grass- and forb-feeders are numerous. Miridae and Cicadellidae are well represented, as are Elateridae. Diptera include a strong representation of Tachinidae and Bombyliidae, many of them cutworm parasites. Many Diptera, Muscidae, Ephydridae, Chironomidae, Culicidae, are associated directly or indirectly with sloughs or temporary pools. The aquatic fauna of the sloughs is rich, and includes a good representation of Trichoptera, Ephemerida, Odonata and Coleoptera, in addition to the groups previously mentioned.

The prairie fauna has some relationship to that of the tundra and of open subarctic regions, as is exemplified by the occurrence of such northern groups as *Oeneis*, *Aspilates*, the *Plebeius aquilo* (Bdv.) group, and *Boloria frigga* (Thun.), to name a few. Species characteristic of the prairies range not only through the aspen parkland, but also far to the north in the open grasslands of the Peace River and Athabaska regions. At Fort Smith, N.W.T., a very high proportion of prairie and parkland forms is found; at Fort Simpson the proportion is much reduced, but still noticeable. Beyond this point a few prairie elements penetrate on eroded hillsides even as far as the Mackenzie delta.

Zonation in the prairies is known to exist, as is evident from some of the types of species ranges already discussed. Precise correlation is, however, lacking. In a general way it can be suspected that some of the species characteristic of southern Manitoba are associates of true prairie (others are woodland or bog associates), that some of those confined to southern Alberta and Saskatchewan depend on mixed prairie, and that species penetrating farther north can succeed in a variety of environments. Evidence of a specific fauna associated with the fescue grassland is less obvious. The aspen parkland contains, as would be expected, a mixture of prairie and boreal insects; so far as known it does not have an endemic fauna.

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